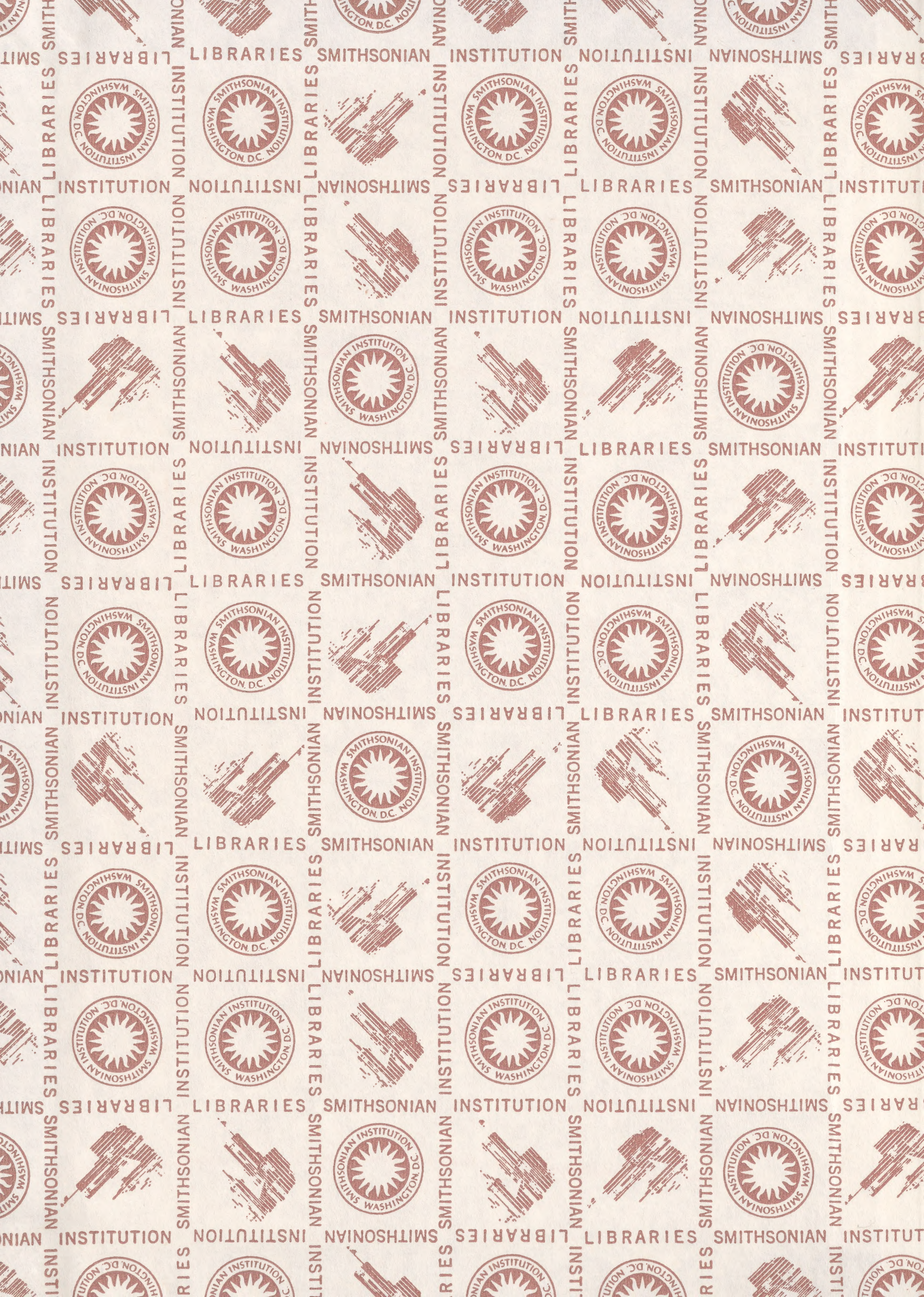
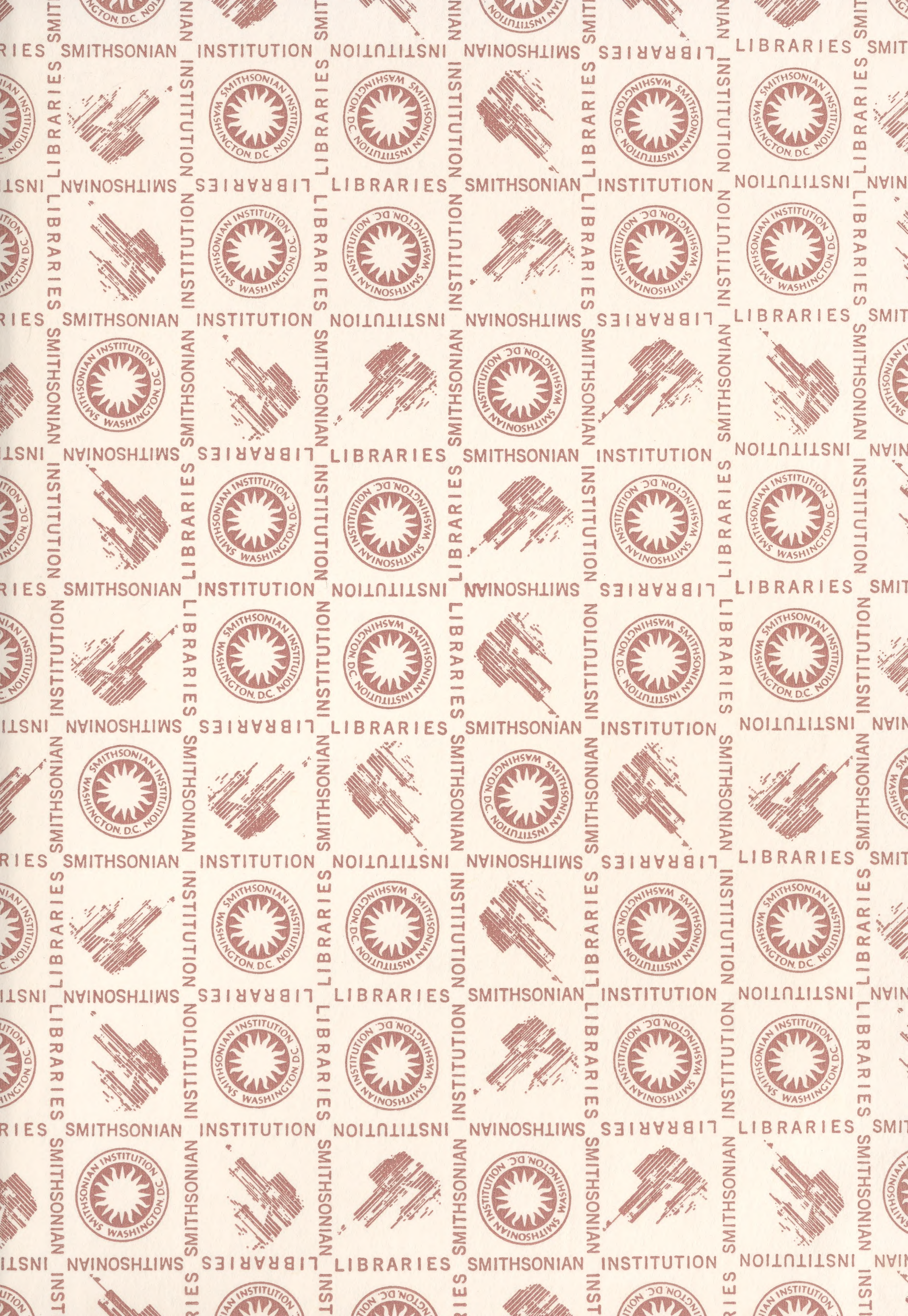


























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OF  
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EDITED, UNDER THE DIRECTION OF THE COUNCIL,

BY

C. R. C. PAUL, M.A., PH.D. with the assistance of R. H. COWIE, B.SC. *and*  
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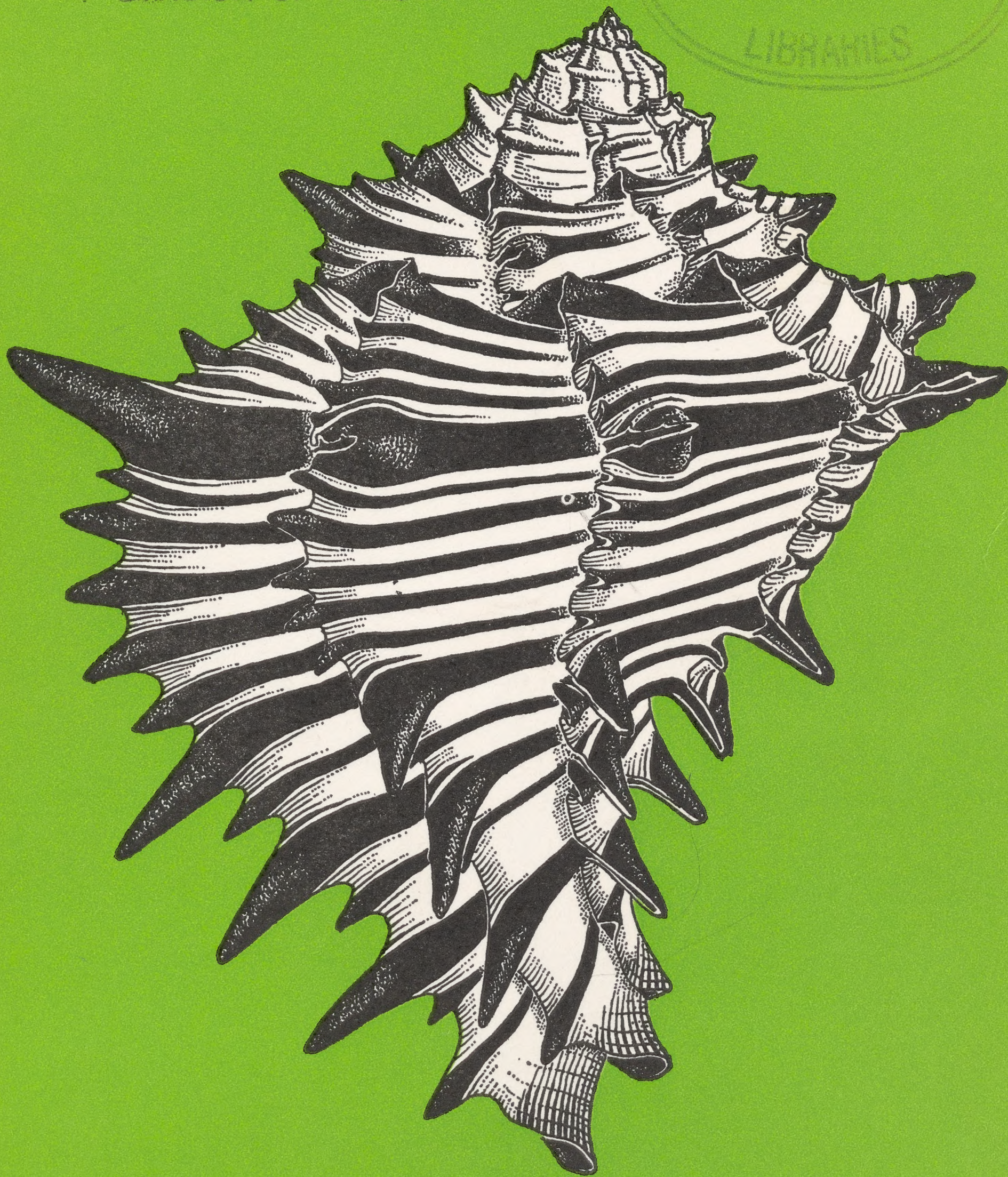
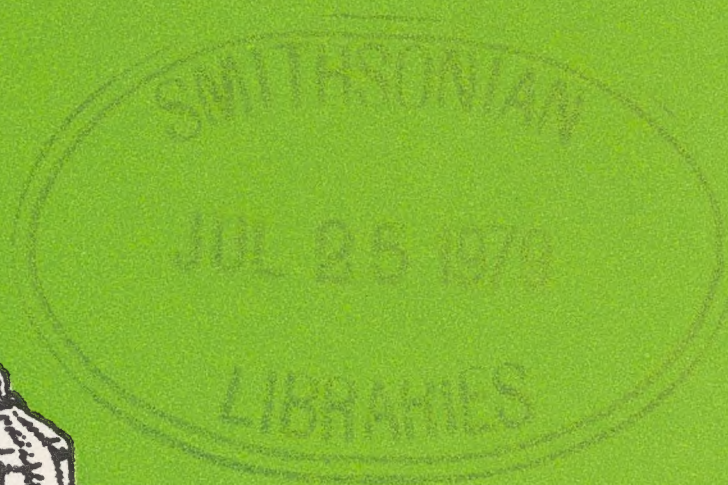
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# MARINE MOLLUSCS IN WALES

JUNE E. CHATFIELD

Zoology Department, National Museum of Wales, Cardiff, CF1 3NP

(Present Address: The Gilbert White Museum and Oates Memorial Library, The Wakes, Selborne, Alton, Hampshire.)

*(Presidential Address, delivered 13 March 1976)*

*Abstract:* The first section of this paper gives a short history of collecting, publishing and study of marine molluscs in Wales from the eighteenth century to the present day. This includes information on the life and work of Thomas Pennant, William Lyons, Lewis Weston Dillwyn, John Gwyn Jeffreys, Edward Donovan, Philip Henry Gosse, Bartlet Span, John Read le Brockton Tomlin and J. Davy Dean; there are also passing references to the contributions of other authors. The second section is divided into small geographical regions and in each there is a short description of the coast, references to relevant publications on the marine molluscs and notes on some species of particular interest. At the back of the paper there is an appendix divided into sections of geographical regions which gives a summary bibliography to the distribution of marine molluscs in Wales.

This paper is an expanded version of my Presidential Address for March 1976. It summarizes the history of collecting and the publication of lists of species of marine molluscs found on the Welsh coastline from the eighteenth century to the present day. A detailed list of references giving published records of distribution data is given in the Appendix. It is hoped that this compilation will provide a useful basis for future studies, especially as there are many areas of coastline for which the marine molluscan fauna is largely unknown. The second part of the paper gives a brief description of the nature of the Welsh coastline together with some information on the marine Mollusca.

## A HISTORY OF COLLECTING

Serious study of the marine molluscs of Wales began in the eighteenth century and this was pioneered by THOMAS PENNANT (1726-1798).

Pennant was born in Flintshire in North Wales: he attended Queen's College, Oxford, but left without taking a degree. Much of his life was centred around North Wales and he travelled extensively both in Wales and elsewhere. These travels provided Pennant with much of the information needed to write books on natural history and travel. Anyone reading accounts of early travels in Wales in the eighteenth century will come to realize what a remote part of the country it was. The very rough state of the roads in the days of horse-coach travel made long journeys something of an act of endurance. These problems, evident in lowland England, were even greater in Wales which is essentially a hilly and mountainous country with a high rainfall. An account of Pennant's travels in North Wales was published in two volumes entitled 'Tour of Wales' in 1778 and 1781, and in these volumes he covers a very broad spectrum of subject matter, but molluscs are only mentioned twice. These include reference to a mussel *Mytilus*



*umbilicatus* Pennant found at Priestholm Island off Anglesey (a species no longer recognized and now synonymized with *Modiolus modiolus* (L.)), and secondly an account of shell-sand being used as a fertilizer on the land on Anglesey (Pennant 1781). Pennant's major contribution to zoology was the publication of his four volume work 'British Zoology' of which the fourth volume included the British Mollusca (Pennant 1777). The scientific names of many of the molluscs have changed since Pennant's time but he did use the Linnean binomial system and he also provided illustrations, so it is possible to update the nomenclature in many cases. In some examples the names have even come through two hundred years of zoology unchanged. Anglesey is often quoted in this work as a locality for marine molluscs and one gains the impression that Pennant collected specimens himself and knew the natural habitats in which the various species were to be found. He shared his interest in natural history with the Morris brothers of Anglesey with whom he kept up a flourishing correspondence (Matheson 1954). Pennant also made a collection of shells and this remained at the family home at Downing Hall, Flintshire until 1913 when it was presented to the British Museum (Natural History) by the Earl of Denbigh. This was a fortunate move, since Downing Hall was burnt down in 1922.

Marine molluscs were also being collected and studied in South Wales in the eighteenth century and early nineteenth century by WILLIAM LYONS (1766–1849) of Tenby. Unlike Pennant, Lyons did not write books on molluscs, but he did make a very extensive collection of marine and non-marine shells. The Lyons collection is now in the Tenby Museum to which it was presented in 1878 by his daughters Jane and Sarah. The non-marine shells in the Lyons collection were reported on by Kennard (1944).

Early collectors were not usually concerned with biological recording and their main interest lay in the differences between species and in acquiring as complete a collection as possible. Thus habitat data are invariably absent and locality data and the date of collection extremely spasmodic on the labels of old collections. The collector would often be able to remember where each shell came from and how it was acquired, but if this information were not written down it would die with the collector.

Many of the shells in the Lyons collection came from Tenby, but there are others from localities outside Wales. Lyons may well have acquired some of these through his frequent correspondence with the leading conchologists of his day. He was sufficiently well known in conchological circles to be honoured with a new genus of bivalve—*Lyonsia*—named after him.

At about this same time and fifty-five miles to the east, LEWIS WESTON DILLWYN (1778–1855) in Swansea was making a shell collection and writing about molluscs. Dillwyn was born in Ipswich, Suffolk but his American-born father was descended from a Breconshire family. L. W. Dillwyn spent most of his life in South Wales where he was head of the Cambrian pottery in the Lower Swansea Valley which was then at the peak of its industrial development. Dillwyn's entry into the pottery was made possible by his father who purchased the lease and a controlling interest on behalf of his son, L. W. Dillwyn (Hughes 1972). As well as his career in the potteries, Dillwyn was also concerned with politics: he was an M.P. from 1832 to 1837 and Mayor of Swansea in 1839. Dillwyn's most well-known conchological publication, 'A descriptive catalogue of Recent shells', is world-wide in its scope (Dillwyn 1817) as was his shell collection but he did collect some shells on the Welsh coast. The L. W. Dillwyn collection is now in the National Museum of Wales. Dillwyn's pottery and natural history interests did come together since the porcelain was often decorated with natural history objects (Hughes 1972) and the draughtsman employed to illustrate his book 'A descriptive catalogue of Recent shells' was the same artist engaged in painting the pottery.

Swansea continued to be a source of conchologists in the nineteenth century. A Swansea man, JOHN GWYN JEFFREYS (1809–1885) wrote one of the standard works on British Mollusca and also made a very large private shell collection. Jeffreys was born in Swansea where he followed the family tradition and worked as a solicitor until 1856, when he was called to the bar and resided in the London area for the rest of his life. He eventually gave up his legal



career to devote all his time to the study of molluscs and during this period of his life he joined many marine collecting expeditions.

Jeffreys lived in Swansea for forty-five years and it was through his collecting trips on the Welsh coast that this remarkable collection was started. In those early years of collecting, Jeffreys was given help and encouragement by L. W. Dillwyn. The Jeffreys collection is now in the National Museum of Natural History, Smithsonian Institution, Washington D.C. It was apparently offered for sale by Jeffreys to the British Museum (Natural History) but the two parties did not reach agreement, whereupon it was promptly bought by William Healey Dall, and shipped to the United States. Dall visited Jeffreys and saw his collection in London in 1878 and in May 1882 Jeffreys (in a letter) offered his collection for sale to Dall at the price of £1,050. A subsequent letter from Jeffreys to Dall includes an outline of the contents of the Jeffreys Collection (Bartsch, Rehder and Shields 1946). The accession files in Washington list an initial purchase of molluscan and brachiopod material from Jeffreys in 1871 with the bulk of the collection arriving in 1883, 1884 and 1885.

Much of the zoogeographical data from the Jeffreys collection is published in the text of his five volume work 'British Conchology' (Jeffreys 1862-1869). Jeffreys acquired the collection of William Turton (1762-1835), author of a number of books on British conchology and as opportunity arose he acquired the collections of other conchologists too (Matheson 1972).

EDWARD DONOVAN (1768-1837), another traveller, like Pennant, with conchological inclinations and a large private income, published a two volume account of his travels in the south entitled 'Descriptive excursions through South Wales and Monmouthshire in the year 1804 and the four preceding summers'. (Donovan 1805). In the second volume there are a number of references to marine molluscs at Oystermouth, Oxwich, Pendine, Tenby, Caldy Island, Stackpole and Milford Haven. Donovan was particularly impressed by the numerous ridges of shells on the sands at Pendine which included some uncommon species. This locality is still an excellent place to collect shells of sandy shores. Donovan also published a five volume work 'British Shells' (Donovan 1800-1804). Like Pennant he amassed a large private collection of natural history objects in London and to which the public were admitted.

Tenby, on the coast of South Wales, was a centre for collecting shells. It was a fashionable small seaside resort and collections were made by holiday visitors as well as by resident conchologists. The opening of the South Wales Railway in the 1850's increased the accessibility of Tenby to visitors, although it was already popular in the pre-railway days (Donovan 1805).

One of the more famous zoological visitors to Tenby was PHILIP HENRY GOSSE (1810-1888) who wrote many books on descriptive zoology. Gosse's stay in Tenby was written up as a book entitled 'Tenby: a seaside holiday' and this is a delightful example of Victorian natural history writing (Gosse 1856). Like most travel books it covered a wide range of subject matter, but there are references to molluscs found on the shore including a lengthy description of the Rock-borer or Red-Noses, *Hiatella arctica* (L.), which is still to be found today at low tide on the Island at Tenby. One of the chapters in a book 'Seaside Studies' (Lewes 1858) was based on Tenby, but unlike Gosse the author gives little information on the precise localities and the molluscs found there. Some of the interest of Victorian visitors in shells is reflected in the presence of a list of local shells included in Mason's Town Guide to Tenby published in 1866.

Many of the eighteenth century and early nineteenth century records of marine molluscs were very incomplete, but towards the middle and latter part of the nineteenth century some fairly extensive check lists were published. Much of this work was made possible by the availability of more complete and detailed reference books (particularly that of Jeffreys) to help with identification.

A list of shells of Tenby and neighbourhood (comprising 178 species and additional varieties) was published by BARTLET SPAN (1833-1917). Span was an Englishman who settled in Tenby on his return from India where he had worked as a civil engineer. During his residence in Tenby he formed a shell collection and from 1894 until just before his death in 1917



he was Honorary Secretary of the Tenby Museum. Span helped to set the museum on a firm financial basis. Span made a thorough study of the local marine Mollusca and also took part in dredging trips: his list of Tenby shells was published in the *Journal of Conchology* (Span 1899). Bartlet Span was a member of the Conchological Society of Great Britain and Ireland and in the proceedings he is recorded as having exhibited specimens at meetings (*J. Conch., Lond.* 9, 181, 218; 11, 152).

Various other papers on the marine Mollusca of the Tenby district were written by holiday visitors: Tye (1874), Milnes (1883), Cundall (1889, 1890) and Williams Vaughan (1905). The latter published some additions to Bartlet Span's list for Tenby. Check lists of this kind often stimulate others to fill in the gaps and to publish their results.

After Pennant's time there were no resident conchologists actively working on the coast of North Wales and the few contributions to the knowledge of the marine Mollusca of that area in the nineteenth century are due to holiday visitors. The first of these was published by the Reverend CARLETON GREENE of Huntingdonshire in 1891 who usefully gives localities after the name of each shell (Greene 1891). In 1892 J. R. le B. TOMLIN (1864–1954) provided a list of additional species found in North Wales and he also included the sea-slugs and cephalopods which Greene did not cover (Tomlin 1892). Tomlin was resident in Wales when he was teaching at Llandaff Cathedral School in Cardiff and it was as a result of his connection in the 1890's with the National Museum of Wales (then known as the Cardiff Museum) that his large world-wide collection of molluscs and conchological library came to Cardiff after his death (Salisbury 1954).

Mochras or Shell Island, near Llanbedr on the extreme northern part of Cardigan Bay, has long been known as a beach where seashells can be found in large numbers and this has evoked comment from various conchologists. Greene (1891) did remark that it was not as good at the time of his publication as it had been in earlier years and nearly twenty years later, Dean (1906) thought that it was grossly over-rated as a collecting site and that Harlech a few miles to the north was far better.

A list of names of shells found on Shell Island was produced by Cotton (1930) and was presumably for sale locally to holiday-makers. Barmouth, some miles south in Cardigan Bay was rated as being a poor collecting place for shells (Moore 1909) as there were few good rocks on the shores and the sands were very exposed and any shells washed up were soon smashed.

J. DAVY DEAN (1876–1937) continued the study of molluscs in Wales in the first part of the present century. Dean was born in Manchester and trained in art at the Manchester School of Art, but he had an early interest in shells and became a member of the Conchological Society in 1897 (Matheson 1937). He moved to Cardiff in 1915 and three years later was appointed as Assistant Keeper in Zoology in the National Museum of Wales where his artistic abilities were used in the preparation of gallery exhibits. Dean remained at the museum until his death in 1937 during which time he worked and published on molluscs. His final paper was a most useful account of the conchological cabinets of the nineteenth century which includes collections relevant to the study of marine molluscs in Wales (Dean 1936). A very well prepared and labelled collection of molluscs made by Davy Dean, which includes some Welsh marine examples, is now in the National Museum of Wales (on long loan from the Newport Museum and Art Gallery).

In the nineteenth century most of the work published on the marine molluscs of Wales was concentrated around a few popular holiday resorts, like Tenby and Swansea which provided good collecting and which were accessible by the transport systems of the time. In the mid-twentieth century most publications on marine molluscs have concentrated around Swansea, the Pembrokeshire coast, Aberystwyth and Menai Bridge and most of this work has been done by the staff and students of the various colleges of the University of Wales, the Marine Science Laboratory at Menai Bridge, the two coastal centres of the Field Studies Council at Dale Fort and Orierton and by various bodies concerned with commercial shell fisheries. Details of these



contributions to the literature appear in the following section and in the Appendix. Additional to these, there is the work of the Conchological Society's marine census which is currently in operation and hopefully this will lead to the publication of maps of the marine molluscs in the not-too-distant future.

#### THE WELSH COAST AND ITS MARINE MOLLUSCA

Wales has a varied coastline providing a good range of habitats for marine molluscs. There are rocky shores, cliffs, sandy shores, mud-flats, estuaries and salt-marshes and there is also a full range of exposures from very rough exposed shores to calm and sheltered bays. The shape of the coastline also gives beaches with a variety of aspects: there are beaches facing north, west and south and a few facing east. In areas where the coastline is incised with many headlands and bays there can be beaches of contrasting aspects in a small area.

There are almost 400 species of marine Mollusca recorded from the Welsh coast and new species are still being added to the list from time to time. This total includes 9 species of Polyplacophora (chitons or coat-of-mail shells), 1 species of Aplacophora (aberrant worm-like molluscs living in sediments offshore), 240 species of Gastropoda (sea snails and sea-slugs), 2 species of Scaphopoda (tusk shells), 130 species of Bivalvia (clams) and 10 species of Cephalopoda (octopus, cuttlefish and squid). Many of these molluscs are to be found living on the shore between the high and low water marks of extreme spring tides, although some of these littoral species will also extend into the sublittoral zone offshore. Other species, however, are entirely confined to offshore waters and are only found alive on the shore when washed up by exceptional storms. The shells of some of the off-shore species, however, form a consistent component of the dead strand-line shells.

The detailed distribution of many species of Welsh marine molluscs is determined by the distribution of suitable habitats and many molluscs are fairly specific in their habitat choice. In contrast there are some species whose distribution in Wales is related to geographical position and especially climatic factors. The Gulf Stream flows close to the south-western shores of the British Isles and results in a warmer sea temperature and this enables molluscs typical of more southern latitudes to live in the south-west of Britain.

The range of species and their relative abundance can fluctuate due to natural factors and a good example of this is the effect of the exceptionally hard winter of 1962-3 on the intertidal fauna (Crisp 1964). In South Wales this caused a reduction in the range of the top shell *Monodonta lineata* (da Costa) which had formerly lived on the Worms Head causeway, Gower (Thompson—personal communication) and at other situations in Glamorgan (Jenkins 1976). Future recording will also be useful in following up the come-back of some of the species lost from former habitats as a result of the 1962-3 winter. At the present time some of the investigations on the fauna of the Bristol Channel and elsewhere in Wales are directed towards monitoring of the populations and detecting possible changes in the fauna due to human factors like pollution. In these situations it is important to understand the amplitude of fluctuations in populations due to natural as well as artificial causes.

The final section of this paper includes an account of the habitats and references to molluscs of small stretches of coast starting in the Bristol Channel. Illustrations of the most common seashells found in Wales are given in Chatfield 1977. A more detailed bibliography appears in the Appendix.

**THE BRISTOL CHANNEL.** In recent years there has been an upsurge in interest in the marine fauna of the Bristol Channel since there is a proposal to build a barrage across the Severn Estuary to harness tidal energy for the production of electricity. Several positions have been suggested for this and it is obvious that there would be marked changes in the marine life above



the barrage. The possible environmental impact is being investigated by the Severn Estuary Study Group. Some of the low shore molluscs, particularly *Macoma balthica* (L.) in the mud flats of the upper estuary, form an important item of food for the populations of wading birds.

Part of a detailed survey of the sub-littoral fauna of the Bristol Channel from Caldy Island to Newport has now been published (Warwick and Davies 1977). By means of grab and dredge samples 155 stations were studied in the Bristol Channel in 1972–1973 and maps made showing the distribution of the different bottom materials. The results were analysed by computer (dendrograms) to group stations which had a similar species composition. In general terms the molluscan communities usually related to the nature of the substratum. Only common species were recorded in this paper. The molluscs found were those whose shells are often cast up on the beaches of Carmarthen Bay and Gower and included: *Philine aperta* (L.), *Nucula tenuis* (Montagu), *N. turgida* Leckenby and Marshall, *Chlamys varia* (L.), *Venus striatula* (da Costa), *Spisula elliptica* (Brown), *Donax vittatus* (da Costa), *Tellina fabula* Gmelin, *Abra alba* (W. Wood), *Pharus legumen* (L.) and *Ensis siliqua* (L.). The most comprehensive published account of the marine Mollusca of the Welsh shore of the Bristol Channel from Kenfig up to the Upper Severn Estuary is that of Boyden, Crothers, Little and Mettam (1977).

**CHEPSTOW TO PORT TALBOT.** This stretch of coast along the south includes some of the more estuarine parts of the Bristol Channel. With the exception of some rocks near the Severn Road Bridge, the coast from the bridge to Cardiff consists mostly of mud flats with some salt-marshes on the upper part of the shore. Here the shoreline is protected by a sea wall. The rivers Usk, Rhymney, Taff and Ely enter the Bristol Channel along this section of coast. Triassic marls outcrop and form cliffs at Penarth Head (which overlooks Cardiff docks) and the shore is made up of marls from Penarth to Sully. In places these marls form ledges on the shore and there is an interesting rocky habitat with abundant brown seaweeds on the causeway to Sully Island. Carboniferous and Liassic Limestone outcrops on the shore at Barry and the coast is mostly bounded by vertical cliffs of horizontally bedded limestone from Porthkerry Park, Barry, westward to the Ogmore estuary, south of Bridgend. In this stretch of coastline the beaches are usually exposed, with limestone pebbles on the top of the shore and mostly weedless limestone platforms below. Llantwit Major beach is one of the better sites for marine molluscs. On the west side of the River Ogmore and up to Port Talbot, the beaches are sandy.

Lists of the marine Mollusca for this coast have been published by Purchon 1947 and 1957 and Boyden, Crothers, Little and Mettam 1977 and by other authors listed in the bibliography (Appendix 1).

In general terms the Chepstow to Port Talbot coast is not rich in species of marine Mollusca, being affected in the upper reaches by low salinity and high turbidity (and hence limited plankton) and in the west by exposed beaches. The muddy shores east of Barry support *Hydrobia ulvae* (Pennant) and mud-dwelling bivalves including *Macoma balthica*. The rocky sections of shore are colonized by the four classic species of *Littorina*, *Gibbula umbilicalis* (da Costa), *G. cineraria* (L.), *Patella vulgata* L., the boring bivalve *Hiatella arctica*, *Mytilus edulis* (L.) and a few other species. At one time *Monodonta lineata* occurred on this stretch of shore (Purchon 1957) but this species was eliminated by the hard winter of 1962–63.

**SWANSEA BAY, GOWER AND THE BURRY INLET.** Swansea Bay has a muddy substratum with some sand and it extends from Port Talbot to the Mumbles where there is also a rocky headland. The southern part of the Gower peninsular consists of rocky headlands (Carboniferous Limestone) and some sandy bays and coves. Oxwich Bay is prolific in molluscs and a good site to collect. Around Port Eynon there are exposed rocky shores with relatively little weed cover although Port Eynon Point offers some shelter. The promontory of Worms Head in the west gives a large expanse of rocky shore and rock-pools rich in marine life which can be reached at low tide. Extending north from Worms Head are the extensive sands of



Rhossili Bay where many marine shells may be found. In contrast, northern shores of the Gower peninsula consist mostly of salt-marshes, mud and sand flats which also extend to the north shore of the Burry Inlet. These flats are the site of the Penclawdd cockle fishery.

This region has a richer molluscan fauna than that to the east. Here the water is fully saline and relatively free of suspended particles of mud. The amount of shelter affects the colonization by littoral molluscs, since the richest collecting sites are the most sheltered and the poorest are the most exposed. The variety of habitats found is partly responsible for the diverse and relatively rich molluscan fauna. A number of specific records of marine Mollusca is given in Jeffreys (1862–1869) for it was here that he did most of his early collecting. The sandy bays at Oxwich and Rhossili are both prolific in shells washed up on the shore, and live specimens are also to be found. A number of shells can also be collected on the muddy shore of Swansea Bay. A typical rocky shore fauna occurs at the Mumbles, Pwll Ddu Bay, the western headland of Oxwich Bay and at the Worms Head, Rhossili, whilst a rather limited fauna occurs on the exposed rocky shore near Port Eynon.

The salt-marshes, mud and sand flats of the Burry Inlet support a limited but specialized fauna while some rocky shore species occur on the harbour walls at Burry Port. References to papers recording the marine molluscs of this section of shore are given in the Appendix.

An oyster fishery was once operative from the Mumbles and the oysters collected by dredging from oyster skiffs. This flourished in the nineteenth century (Matheson 1934). On both shores of the Burry Inlet there was an active cockle fishery and, although now declining, the industry is still operative at Penclawdd on Gower. The cockles are gathered from the sand flats reached at low tide by horse and cart and they are processed for market in small factories in Penclawdd. Further details of this cockle fishery are given in Jenkins, G. 1976.

**CARMARTHEN BAY.** Three large estuaries, the Gwendraeth, Afon Tywi and Afon Taf enter the sea on the east side of Carmarthen Bay and these rivers contribute to deposits of muddy shores. There are salt-marshes near Laugharne and in a few other localities. West of Ginst Point is a large expanse of sand exposed at low tide which includes the Laugharne and Pendine Sands: this is a good locality for collecting marine molluscs. The shore is backed by sand-dunes at Pendine Sands but to the west of Pendine, the shore is bounded by fairly vertical Carboniferous Limestone cliffs with boulders beneath. Millstone Grit outcrops on the shore near Marros beach whilst Saundersfoot Bay (from Telpyn Point to Monkstone Point) is cut into sandstones of the Coal Measures, which in some places give a cliffed coast-line. To the south of Saundersfoot harbour are cliffs with some boulders on the upper shore and a sandy beach below. Millstone Grit outcrops again on the shore from south of Monkstone Point to North Beach in Tenby. Castle Hill, Tenby and St Catherine's Island are made of Carboniferous Limestone, but the beach below is mostly sandy. South of Tenby there are extensive sands and a sand-dune system on the landward side of the shore. Carboniferous Limestone rocks occur on the shore again to form rocky headlands at Giltar Point and at Lydstep Point. The sands at Pendine, Saundersfoot and Tenby are good collecting sites for marine shells. Razor shells (of several species) are particularly common at Saundersfoot and on the harbour wall there is a warning notice to holiday-makers which reads 'Watch your step—Razor Shells'. The Razor Shells at Saundersfoot are collected by local people for fishing bait and it is possible that this could deplete the intertidal populations.

The cliffs of Carmarthen Bay provide habitats for species like *Littorina neritoides* (L.) and *L. saxatilis* agg. which are characteristic of crevices in rocks of the upper shore. Where limestone rocks outcrop low on the shore, as on St Catherine's Island at Tenby, there are various species of rock-boring bivalves, in addition to mussels (*Mytilus edulis*) and Dog-whelks (*Nucella lapillus* (L.)) which live on the surface of the rocks.

The rich molluscan fauna for this part of the coast is reflected in the extensive list of marine species published by Bartlet Span (Span 1899). A number of these include off-shore species



washed up on the beach or collected by dredging. Many of the publications concerning the marine Mollusca of this region date from the nineteenth century, so there is a need for up-dating the records. A full list of publications is given in Appendix I.

Commercial shell-fishing was once operative in Carmarthen Bay. Cockles were collected on the sands near Laugharne and the cockle-processing huts on the shore at Laugharne have only recently been demolished. In the nineteenth century oysters were dredged from off Caldy Island (Donovan 1805).

**THE PEMBROKESHIRE PENINSULA.** This region includes Manorbier in the south-east, Milford Haven and the Angle peninsula to the south, the Dale area, Skomer and other islands off shore, St Brides Bay, St David's Head, Strumble Head, Fishguard, Newport Sands and the shore along to Cemaes Head at the mouth of the Teifi, which marks the southern limit of Cardigan Bay.

Much of the northern part of this region, north of St David's is composed of old sedimentary rocks (slates and shales) of Cambrian, Ordovician and Silurian age. These rocks contribute to give a scenic cliffed coastline with rocky shores. In some localities the rocks descend steeply to the beach and provide only a limited extent of rocky habitat. Below the cliffs the beaches consist of grey sand, shingle and some small boulders. Newport Sands is the most extensive sandy beach in the northern part of the Pembrokeshire peninsula and shells are abundant on the strandline. Some igneous rocks outcrop on the shore, particularly on headlands like St David's Head and Strumble Head, forming steep cliffs and relatively inaccessible rocky shores. South of St David's Head is a sandy beach, at Whitesand Bay.

To the south of St David's there are mostly younger rocks of Devonian and Carboniferous age. St Brides Bay is cut into sandstones of the Coal Measures and the shore is an extensive sandy beach with some cliffs to the south.

Old Red Sandstone rocks occur at St Brides, both northern and southern shores of Milford Haven and at Manorbier; in many localities they give rise to rocky shores. The island of Skomer and the rocky headland adjacent to it are formed of igneous rocks, with some sedimentary Silurian rocks on the mainland. Sandy beaches occur at Musselwick Sands, Marloes Sands and Dale. The shores of the Angle peninsula are composed either of Old Red Sandstone (in the north) or of Carboniferous Limestone (in the south): in some stretches these rocks provide a cliffed shoreline with rocky beaches. A good rocky shore with rockpools and seaweed is found on the limestone shore to the north of West Angle Bay where a rich molluscan fauna can be found at low spring tides. On the sheltered, gently sloping shores of Milford Haven, there are rocks and stable boulder beaches (e.g. Angle Point), mudflats and salt-marshes. Outside the haven there are sandy beaches at Freshwater West, Broad Haven (near Bosherton), Freshwater East and Manorbier. These sandy beaches are all some-what exposed. At Manorbier there is also a rocky intertidal platform of Old Red Sandstone.

The Pembrokeshire peninsula provides a wide range of habitats for marine molluscs. As it is the most south-westerly extension of Wales, the sea temperature is influenced by the warm waters of the Gulf Stream and many species of marine molluscs with a southerly bias in their geographical distribution in the British Isles occur abundantly on the Pembroke coast. This rich molluscan fauna has been studied by the two field centres at Dale Fort and Orielson, and also by numerous visiting parties. Crothers (1966) lists 314 species of marine molluscs in the Dale Fort faunal list. The Pembrokeshire shores represent a wide range of conditions of shelter and exposure and it was here that Ballantine worked out his exposure scale for rocky shores (Ballantine 1961). An offshore survey is currently in progress studying the fauna of the Celtic Sea from the Pembroke coast towards the south coast of Ireland. This survey is being done by the staff of the Oil Pollution Research Unit based at Orielson. An annotated list of publications and University theses concerning the marine Mollusca of the Pembroke peninsula is given in Appendix I.



The sandy beaches are variable as collecting places for shells. Shells are plentiful at Newport Sands and Newgale Sands (where *Donax vittatus* dominates), but less plentiful and often broken at Manorbier, Freshwater West and Whitesand Bay. In some instances the pockets of shells in the strand-line can yield many of the smaller species (*Rissoa*, *Alvania*, *Cingula* etc.). The widest range of rocky shore species is found on fairly gently sloping, sheltered shores, where there are rocks at all levels of the shore. Many of the beaches, however, are backed by steep cliffs which only support the upper shore molluscan fauna, and there are often no rocks on the lower shore.

The geology in this part of the Welsh coastline is very varied and the different rocks affect surface texture and the abundance of crevices. Limestone is a particularly suitable surface for marine molluscs, since there are many stable crevices and bivalves can also burrow into it. In contrast, the slates and shales of the northern part of the peninsula often provide too smooth a surface and the crevices are unstable due to the crumbling nature of the shale lying between the slate. The more limited rocky shore fauna of the slate and shale coasts is comparable with the situation in Cardigan Bay.

**CARDIGAN BAY.** This section of coast comprises the Marine Census Area 22 and it extends from Cemaes Head near Cardigan in the south, north to Porthmadog and along the south coast of the Llyn peninsula to Bardsey Island.

In the southern half of Cardigan Bay from Cemaes Head to the Dyfi estuary, the coast is mostly bounded by steep cliffs composed of slates and shales of Ordovician and Silurian age and in many places there is limited access to the shore. In this region the cliffs are usually steep and the beaches below consist of shingle, with expanses of sand exposed at low tide. In some places rocky outcrops and boulders occur low on the shore. Although the cliffs are composed of bedrock in most areas, in some localities (e.g. north of Aberaeron) the cliffs are lower and consist of loose solifluction material (pieces of rock in an earthy matrix) which was deposited comparatively recently in the Pleistocene Period. Details on 24 beaches in Cardigan Bay (with information on access) are given by Roberts 1976. North of Aberdyfi the bedrock consists of a range of coarse to fine-grained rocks (conglomerates, grits and shales) of Cambrian age. These outcrop on the shore between the Dyfi and Mawddach estuaries, but much of the shore-line in the north of Cardigan Bay including Ynyslas, Tywyn, Dyffryn and Harlech is bounded by sand-dunes and in this area most of the beaches consist of exposed stretches of sand. Estuarine conditions with intertidal mud flats and some salt-marshes occur in the Teifi, Dyfi and Mawddach estuaries and around the inlet on which Porthmadog is situated.

The southern shore of the Llyn peninsula consists mostly of sandy bays with a shore-line often bounded by sand-dunes and by small cliffs of glacial drift or head material in some localities. On the southern tip of the peninsula around Aberdaron, at St. Tudwal's peninsula and in some other localities, there are headlands with rocky shores below. In the extreme west, the cliffs consist of metamorphic schists and gneisses, whilst St. Tudwal's peninsula is capped by a range of fine to coarse-grained rocks of Cambrian age. At various localities along the south coast of the Llyn peninsula rocky shores are composed of a variety of intrusive igneous rocks.

Cardigan Bay is not a particularly rich area for marine molluscs. Walton (1913) lists 47 species for this part of the coast and Horsman (1922) was able to add 13 further species to the list, making a total of 60 species for the central and southern parts of Cardigan Bay. More recently, Evans (1949) lists 81 species of marine molluscs for the Aberystwyth area. Cotton (1930) lists 209 species of marine molluscs from Mochras and the shores of Cardigan Bay, but a number of these were probably based on dead shells, washed up on the shores of Shell Island rather than records of living animals taken *in situ*. Most of the publications on the marine molluscs of this region have taken the form of ecological studies on the relatively few common species occurring in the area around Aberystwyth which include the rocky shore fauna and also species of muddy habitats from the Dyfi estuary. The exposed nature of the shore of Cardigan Bay is one of the major factors controlling the numbers of species of marine molluscs which occur



there. In addition there is limited variety in the inter-tidal habitat. Much of the rocky habitat consists of cliff face and there are relatively few weed-covered rocky shores and also few rocks exposed on the lower shore so that only the upper rocky shore fauna is well represented. In many areas the smooth nature of the rocks does not encourage a rich molluscan fauna, since there are usually fewer stable crevices to provide shelter for marine molluscs than in a rock like limestone. Possibly as a result of the limited nature of the collecting, Cardigan Bay has not been adequately surveyed for inter-tidal marine molluscs and future field work could usefully add to our knowledge of the marine molluscs of this section of the Welsh coastline.

Although the inter-tidal fauna of Cardigan Bay is limited, the extensive list of shells recorded on the shell beach at Mochras (Cotton 1930) is indicative of additional species living off-shore. Off-shore studies in Cardigan Bay have been undertaken from the University College of Wales, Aberystwyth and the distribution of many marine species of molluscs assessed (Haward 1977). Many of these are species whose shells are often found on beach strand-lines.

Shell fisheries for mussels, cockles and winkles have been operative in Cardigan Bay, but at the present time it is the Queen Scallop, *Chlamys opercularis* (L.), which is usually harvested by dredging off-shore.

**NORTH WALES.** This region includes the northern shores of the Llyn peninsula, the southern shore of the Menai Straits, Conwy Bay, Great Ormes Head, Colwyn Bay and the Dee estuary, which forms the northern boundary between England and Wales. Much of this coastline faces north-west although some areas (e.g. Llyn peninsula) are exposed whilst others (e.g. the Menai Straits) are more sheltered. The island of Anglesey is included in a separate section.

The southern half of the north shore of the Llyn peninsula, up to Nefyn, includes rocky shores composed of schists and gneisses which provide cliff and rocky habitats with occasional rock-pools. In some areas, including Porth Oer (locally known as Whistling Sands), Porth Colmon, Porth Dinllaen and Porth Nefyn, there are extensive stretches of sandy beaches which are bounded on the landward side by cliffs of unconsolidated head material. Rocky cliffs usually occur forming headlands at the lateral limits of the sandy bays. On some of the beaches there are stable boulders colonized by seaweeds which provide a rocky substratum.

Immediately north of Nefyn the shore-line alternates between cliffs of soft head material and steep rocky cliffs of igneous bedrock, which are often inaccessible. North of Trefor the shore is mostly backed by cliffs of head material, but in some places (e.g. west of the pier at Trefor) Ordovician slates outcrop on the beach forming rocky shore and cliff habitats. The beaches in this region and up to Dinas Dinlle consist of pebbles at the top of the shore with sand exposed at low tide and there may be local accumulations of stable boulders.

Muddy substrata occur in the Menai Straits although in some areas there may be gently sloping exposures of bedrock.

Along Conwy Bay there is generally a low shore-line. Shingle accumulates at the top of the beaches and sands are exposed at low tide. Steep cliffs of Carboniferous Limestone occur around Great Ormes Head, to the north-west of Llandudno. The shore-line at Llandudno and Colwyn Bay is mostly bounded by the promenades of the coastal resorts with a shingle upper shore and sand exposed at low tide. Local patches of salt-marsh occur in the mouth of the Conwy, to the east of the Point of Air and along the shores of the Dee estuary.

Malacologically this is a region of great contrasts. Most of the rocks occur near the top of the shores, so it is the upper rocky shore fauna which is best represented. The shells on many of the beaches are washed up from off-shore populations and many of the species do not occur intertidally. These off-shore populations have been studied for the Llyn peninsula (Dobson, Evans and James 1971) and for Colwyn Bay (Lingwood 1976).

There is considerable variation in the quantities of shells washed up on the sandy beaches on the Llyn peninsula. The two most detailed check lists which include localities in this region are



those of Greene (1891) and Tomlin (1892), although other more recent papers give lists of shells found in individual localities. The work of the Coastal Surveillance Unit, based at the Marine Laboratories, Menai Bridge, includes regular study of two stations on the Lleyn peninsula and three on the southern shore of the Menai Straits. Most of the studies on the Dee estuary have been based on the English side. In general terms there has been very little information published on the marine Mollusca of the Lleyn peninsula and the southern shores of the Menai Straits and most attention has been concentrated on the resorts of the north coast.

Mussels are collected from natural populations in the Conwy estuary and there is a laboratory of the Ministry of Agriculture, Fisheries and Food at Conwy which undertakes laboratory culture and research on commercially important shellfish.

**ANGLESEY AND THE MENAI STRAITS.** The island of Anglesey is situated off the coast of the north-west corner of Wales from which it is separated by the Menai Straits which are only a quarter of a mile in width at Menai Bridge. Anglesey is almost 30 miles in diameter and has a very varied coastline made up of igneous, metamorphic, sedimentary and superficial rocks.

The northern and western shores consist mostly of schists and gneisses which form tall and scenically attractive cliffs around Holyhead. The cliffs and headlands provide rocky shore habitats and between them are many sandy coves. Igneous rocks outcrop in a few places on the western shore and also on the southern mainland shore of the Menai Straits. The rocks on the eastern shore are mostly Carboniferous Limestone with some Old Red Sandstone and Ordovician slates and shales. This eastern shore is the most sheltered and is indented by several bays of which the largest is Red Wharf Bay. The coastline is flatter around Beaumaris and the Lavan Sands, while the northern shore of the Menai Straits is a gently shelving rocky shore with a good cover of brown seaweed. The marine biological station is situated at Menai Bridge. Extensive sand-dune systems occur on the shore on the south-west coast. There are also some coastal outcrops of boulder clay. The substratum off-shore in the Menai Straits is mud.

The shore of Anglesey provides a wide range of habitats including mud, sandy bays and coves and rocky shores representing a range of rock types. Some of these rocky shores provide habitats for crevice faunas and these have been the subject of special investigation (see Appendix). There is also an interesting contrast between the faunas of the more sheltered east coast compared with the less sheltered west coast. Anglesey is a rich site for marine molluscs and has attracted the attention of early naturalists like Thomas Pennant (eighteenth century) and more recently as a base for a marine biological station.

No basic check-list has, so far, been published for the marine molluscan fauna of Anglesey, although two old lists for North Wales (Greene 1891 and Tomlin 1892) give a number of Anglesey records. The most recent list (which includes some sites in North Wales in addition to Anglesey) is that produced by the Coastal Surveillance Unit (Fletcher and Jones 1976) which records over forty species of marine molluscs. Results of off-shore survey work have been published by Dobson, Evans and James 1971. Puffin Island off Anglesey was once used as a marine station for the Liverpool Marine Biological Committee and as a result of this some lists of its molluscan fauna have been published (Archer 1892; Herdman and Clubb 1892).

The majority of the references included in the appendix for Anglesey are lists from single localities or are based on individual species. Most of the recent work on the marine life of Anglesey has been undertaken by M.Sc. and Ph.D. students based at the Marine Science Laboratories at Menai Bridge.

At Tal-y-Foel, on the south shore of Anglesey there is a commercial shell-fish hatchery and also at this site are field trials of shell-fish culture operated by the Ministry of Agriculture, Fisheries and Food. Two species not native to the region, the Pacific Oyster *Crassostrea gigas* (Thunberg) and the Quahog *Mercenaria mercenaria* (L.) are cultured in mud layings.



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## APPENDIX: ANNOTATED BIBLIOGRAPHY

Since most people who study Welsh marine molluscs, whether as amateurs or professionals, tend to work within a particular region, the larger part of the bibliographic list has been divided into geographical regions for ease of use. In addition there is also a list of general references which are not specific to a particular region. The references in these lists are arranged by author in alphabetical order and each entry is annotated to indicate the extent of the zoogeographical information on marine molluscs in the reference. The annotations only refer to the distribution records and in many cases this aspect is only incidental to the main theme of the publication. Some publications refer to several parts of the Welsh coast and these are repeated in each regional section where relevant and the annotations written specifically for the region in which the reference is placed.

Most of the entries in the bibliographic list are published papers, usually in scientific journals. However, a number of unpublished M.Sc. and Ph.D. theses has also been included since many of them contain valuable lists and sometimes off-shore surveys which include information not otherwise obtainable from published sources. These theses may be consulted in the libraries of the University Colleges of the University of Wales and also in the Welsh National Library at Aberystwyth.

Some additional records of marine Mollusca in Wales are to be found in the various reports of the Marine Recorder published in the *Journal of Conchology*, mostly from 1964 onwards.

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- MARSHALL, J. T., 1893–1917. Additions to 'British Conchology'. *J. Conch., Lond.* 7, 241–265, 379–385; 8, 338–372, 385–395; 9, 61–74, 120–138, 165–171, 222–232, 284–296, 332–338; 10, 122–128, 190–193; 13, 179–190, 192–209, 223–231, 294–306, 324–338; 14, 33–35, 65–77, 124–128, 182–190, 200–213, 324–329; 15, 44–47, 87–89, 168–174, 198–203. Almost all the papers contain locality records of marine molluscs in Wales.
- McMILLAN, N. F., 1968. *British shells*. Warne, London. A guide to identification.
- McMILLAN, N. F., 1977. *The Observer's book of Seashells of the British Isles*. Warne, London. A guide to identification.
- PENNANT, T., 1777. *British Zoology 4*. Eyres, Warrington and London. This includes a number of records of marine molluscs from specific Welsh localities.
- TEBBLE, N., 1976. *British bivalve seashells*. H.M.S.O. Edinburgh. A guide to identification. Locality information is given for all the shells illustrated, and a number of these are from Wales.
- THOMPSON, T. E. and BROWN, G. H., 1976. *British opisthobranch molluscs. Synopses of the British Fauna (New Series) No. 8*. Linnean Society of London and Academic Press, London. A guide to identification and distribution of seaslugs and bubble shells.

## CHEPSTOW TO PORT TALBOT. (Counties of Gwent, South and Mid Glamorgan) Marine Census Area 21.

- ANON. 1929 Recorder's Report (Marine Mollusca) *J. Conch., Lond.* 18: 300. Records *Mytilus galloprovincialis* Lamarck as abundant in Cardiff Docks.
- BOYDEN, C. R., CROTHERS, J. H., LITTLE, C. and METTAM, C., 1977. The intertidal invertebrate fauna of the Severn Estuary. *Fld. Stud.* 4: 477–554. This paper includes a useful species list of marine Mollusca with notes on localities and other points of interest. It is the most comprehensive list for the area, recording some 63 species of marine molluscs from the Welsh side of the Bristol Channel.
- BOYDEN, C. R. and RUSSELL, P. J. C., 1972. The distribution and habitat range of the brackish water cockle (*Cardium (Cerastoderma) glaucum*) in the British Isles. *J. Anim. Ecol.* 41: 719–734. *Cerastoderma glaucum* (Poiret) (= *C. lamarcki* (Reeve)) is recorded for Aberthaw.
- BROUGH, M. C., DELHANTY, J. E. and THOMPSON, T. E., 1960. An ecological study of a brackish water pool at Lamby, near Cardiff. *Trans. Cardiff Nat. Soc.* 90: 4–19. *Hydrobia ulvae* and *Limapontia depressa* Alder and Hancock, are recorded.
- BROUGH, J., MATHESON, C. and JEFFERSON, G. T., 1960. *Zoology*. In REES, J. F. (Ed.), *The Cardiff Region, a survey*. University of Wales Press, Cardiff. pp. 58–74. A general account of the shore and its fauna with a few references to marine molluscs.
- CROTHERS, J. H., 1971. Further observations on the occurrence of 'teeth' in the dog-whelk *Nucella lapillus*. *J. mar. biol. Ass. U.K.* 51: 623–639. A list of populations studied is given with localities and date of collection (1969–70).
- , 1974. On variations in *Nucella lapillus* (L.): shell shape in populations from the Bristol Channel. *Proc. malac. Soc. Lond.* 41: 157–170. Nine localities are given for *Nucella lapillus* in this region.
- HADERLIE, E. C. and CLARK, R. B., 1959. Studies on the biology of the Bristol Channel XIX. Notes on the inter-tidal fauna of some sandy and muddy beaches in the Bristol Channel and Severn Estuary. *Proc. Bristol Nat. Soc.* 29: 459–468. Records *Macoma balthica* and *Hydrobia ulvae* from Peterstone Wentloog. There are some descriptions of marine habitats on the Welsh shores of the Bristol Channel.
- HEPPER, H. T., 1957. Notes on *Mytilus galloprovincialis* Lamarck in Great Britain. *J. mar. biol. Ass. U.K.* 36: 33–40. Reports on mixed populations of *Mytilus edulis* and *M. galloprovincialis* at Cardiff and Aberthaw. There was a fairly high percentage of *M. galloprovincialis* at Aberthaw.



- IRELAND, M. P. and WOOTTON, R. J. 1977. Distribution of lead, zinc, copper and manganese in the marine gastropods, *Thais lapillus* and *Littorina littorea* around the coast of Wales. *Environ. Pollut.* **12**: 27–41. The heavy metal content of the shell and body of the two species of molluscs were measured from samples taken at Penarth.
- JENKINS, M., 1976. *The distribution of littoral fauna and flora along the coast of Glamorgan*. County of South Glamorgan (Education Office) 23 pp. Includes an annotated list of marine molluscs found at Sully, Rhose and Sker with an introduction to the habitat.
- KING, P. E. and OSBORN, A., 1969. Oyster dredging. *Gower* **20**: 76–81. Refers to oyster beds at Porthcawl.
- LITTLE, C. and NIX, W. 1976. The burrowing and floating behaviour of the gastropod *Hydrobia ulvae*. *Est. coast. mar. Sci.* **4**: 537–544. Refers to a population of *Hydrobia ulvae* at Barry.
- NATURAL ENVIRONMENT RESEARCH COUNCIL, 1972. *The Severn Estuary and the Bristol Channel: an assessment of present knowledge*. N.E.R.C. Publications. Series C, No. 9., 20 pp. A summary of all aspects of the environment with a full list of references. It includes current research projects, some of which involve molluscs.
- NICKLESS, G., STENNER, R. and TERRILLE, N., 1972. Distribution of cadmium, lead and zinc in the Bristol Channel. *Mar. Pollut. Bull.* **3**: 188–190. High levels of heavy metals are reported in marine molluscs (*Patella*, *Nucella*, *Littorina* and *Mytilus*) in the eastern part of the channel including the shores of the islands of Flatholm and Steephholm. Other sampling sites were: Sully Island, Fontygary Bay and Sker Head.
- PURCHON R. D., 1948. Studies on the biology of the Bristol Channel XVII. The littoral and sublittoral fauna of the northern shores near Cardiff. *Proc. Bristol Nat. Soc.* **27**: 285–310. This paper includes lists of the marine molluscs and ecological notes for Peterstone Wentloog, Barry, Sully Island and Breaksea Point.
- , 1957. Studies on the biology of the Bristol Channel XVIII. The marine fauna at five stations on the northern shores of the Bristol Channel and Severn Estuary. *Proc. Bristol Nat. Soc.* **29**: 213–226. Lists and ecological notes for Portskewett near Chepstow, Llantwit Major and Kenfig.
- REES, C. B., 1939. The plankton in the upper reaches of the Bristol Channel. *J. mar. biol. Ass. U.K.* **23**: 397–425. This includes a useful description of the physical environment with the results of a year of monthly plankton samples. The molluscs receive little attention and are only identified to class level. There are relatively few species in the plankton fauna as a whole.
- , 1940. A preliminary study of the ecology of a mud-flat. *J. mar. biol. Ass. U.K.* **24**: 185–199. The paper describes the results of a transect worked across the shore at a site between the Rhymney estuary and Peterstone Wentloog, just east of Cardiff. High densities of 50–18,100/metre<sup>2</sup> were recorded for *Hydrobia ulvae* and densities of 140–800/metre<sup>2</sup> for *Macoma balthica* living in stiff mud. *Scrobicularia plana* (da Costa) was represented by dead shells only.
- SEVERN ESTUARY CONSERVATION GROUP, 1978. *The Severn Estuary. A heritage for wildlife*. Severn Estuary Conservation Group. A general account of the natural history of the estuary (illustrated in colour) with references to *Hydrobia ulvae* and *Macoma balthica*. The future of the estuary is discussed.
- SEVERN ESTUARY STUDY GROUP, 1977. *Environmental effects of a Severn Estuary Barrage. An appraisal of present knowledge and future research*. Severn Estuary Study Group. This is mostly a description of the environment.
- SMITH, S. T., 1967. The ecology and life history of *Retusa obtusa* (Montagu) (Gastropoda, Opisthobranchia) *Can. J. Zool.* **45**: 397–405. This paper describes a living population of *Retusa obtusa* (Montagu) from mud in Barry harbour. It also records the presence of *Hydrobia ulvae*, *Macoma balthica* and *Scrobicularia plana*.
- TAYLOR, D. A. J., 1971. Shelling in Glamorgan and Pembrokeshire (Census Area 21) and Scilly Isles (Census Area 19). *Conchologists' Newsletter* **39**: 234–240. Some additional records of marine molluscs from this area obtained by diving at Llantwit Major and Breaksea Point. An indication of abundance is given for each species recorded.
- WARWICK, R. M. and DAVIES, J. R., 1977. The distribution of sublittoral macrofauna communities in the Bristol Channel in relation to the substrate. *Est. coast. mar. Sci.* **5**: 267–288. This paper is based on off-shore dredge samples taken in 1972 and 1973 and it includes a number of stations in the Bristol Channel west of Newport. The nature of the bottom material was shown to be an important factor in the distribution of marine molluscs. Only the most common species were listed.
- WOTTON, F. W., 1891. *The marine molluscan fauna of Cardiff*. Handbook for Cardiff and District. British Association. pp. 185–187. A list of some 25 species of marine molluscs with notes on abundance, habitats and localities.
- YONGE, C. M. and LLOYD, A. J., 1939. Studies on the biology of the Bristol Channel III. The shore fauna of Steep Holm. *Proc. Bristol Nat. Soc.* Ser. 4, **8**: 477–478. A rocky shore with a limited molluscan fauna including three species of *Littorina*, two species of *Patella* and *Buccinum undatum*.

#### SWANSEA BAY, GOWER AND THE BURRY INLET. (Counties of West Glamorgan and Dyfed) Marine Census Area 21

- ANON., 1967. Ecology of the shore at Oxwich Bay, South Gower. *Bios*, **1**: 12–26. Results of transects worked across rocky and sandy habitats at Oxwich. Seven species of molluscs were recorded from the rocky shore and 13 species from the sandy shore.
- ANON., 1968. Ecology of the shore at Oxwich Bay, South Gower. *Bios*, **2**: 22–31. *Montacuta ferruginosa*, (found commensal with the heart urchin *Echinocardium cordatum*), *Venus striatula*, *Ensis* sp., *Donax vittatus*, *Tellina tenuis* and *T. fabula*



- were recorded from shore transects. A series of kite diagrams show the seasonal distribution of *Tellina tenuis* at Oxwich.
- BATE, C. S., 1850. Notes on the fauna of Swansea and the neighbourhood, made during the summer of 1849. *Rep. Swansea Lit. Soc.* (1850): 23–35. This paper includes a list of fifteen marine molluscs with notes on the various species. The opisthobranchs are figured (Plates I and II).
- BOWERS, E. A., 1969. *Cercaria bucephalopsis haimeana* (Lacaze-Duthiers, 1854) (Digenea: Bucephalidae) in the cockle, *Cardium edule* L. in South Wales. *J. Nat. Hist.* 3: 409–422. This paper describes a study on 3-monthly samples of cockles collected from Llanrhidian Sands, Gower during 1963–1964. The infection of the cockles by the larval fluke was investigated.
- BRUNT, A. M., 1967. Recolonization with particular reference to Cirripedes of an artificially created land-slide type surface at Three Cliffs Bay. *Bios*, 1: 58–66. Details are given on the recolonization of the bare rock by *Patella vulgata* from monthly studies over one year at Pobbles Bay near Three Cliffs Bay, Gower. *Littorina saxatilis* agg., *L. neritoides*, *Nucella lapillus* and *Mytilus edulis* were also recorded from rocks in the vicinity.
- BURTON, J. C., 1969. Desiccation and inter-tidal zonation in *Littorina* spp. *Bios*, 3: 58–65. The four classic species of winkles are recorded for the Mumbles.
- CHATFIELD, J. E., 1976. Sacoglossans again! *Conchologists' Newsletter* 57: 502. *Limapontia depressa* and *Alderia modesta* were found at Llanrhidian Marsh in October 1975.
- and THOMPSON, T. E., 1975. Recording marine molluscs from the Gower coast, South Wales, 1974. *Conchologists' Newsletter* 53: 438–440. Lists of marine molluscs found on a field meeting to Oxwich Bay and Rhossili.
- and ———, 1976. Field meeting recording marine molluscs from the Gower coast, South Wales, 1975. *Conchologists' Newsletter* 57: 504–506. Lists of marine molluscs found during a field meeting to Rhossili, Llanrhidian Marsh and some other localities on Gower visited by participants of the field meeting.
- COLE, H. A., 1949. Swansea Bay—Mumbles area oyster fishery, and on the possibilities of reviving oyster culture in the River Cleddau, Pembrokeshire. *Report of the South Wales Sea Fisheries District Committee* 1–14.
- CROTHERS, J. H., 1971. Further observations on the occurrence of 'teeth' in the dog-whelk *Nucella lapillus*. *J. mar. biol. Ass. U.K.* 51: 623–639. A list of populations of *Nucella lapillus* visited in 1969–1970.
- , 1974. On variations in *Nucella lapillus* (L.): shell shape in populations from the Bristol Channel. *Proc. malac. Soc. Lond.* 41: 157–170. Lists some localities for *Nucella lapillus* on Gower and at Burry Port.
- DARE, P. J., 1966. The breeding and wintering population of the oystercatcher (*Haematopus ostralegus*) in the British Isles. *Fishery Invest. Lond. Ser. 2*, 25 (5): 1–69. This paper includes the feeding of oyster catchers on cockles in the Burry Inlet.
- DAVIDSON, P. E., 1967. A study of the oystercatcher (*Haematopus ostralegus* L.) in relation to the fishery for cockles (*Cardium edule* L.) in the Burry Inlet, South Wales. *Fishery Invest., Lond. Ser. 2*, 25 (7): 1–28.
- DONOVAN, E., 1805. *Descriptive excursions through South Wales and Monmouthshire in the year 1804 and the four preceding summers*. F. and C. Rivington, London. 2 vols. A mention of *Mytilus incurvatus* Pennant (now regarded as a form of *M. edulis*) at Oystermouth, and shells on the strand-line at Oxwich.
- DRINNAN, R. E. and COLE, H. A., 1957. Oystercatchers (*Haematopus ostralegus*) as pests of cockle and mussel beds. *Nature Wales* 3: 499–503. Survey work on the feeding habits of oystercatchers suggested that they were not a serious pest on the Burry Inlet cockle population.
- FARROW, G. E., 1972. Periodicity structures in the bivalve shell: analysis of stunting in *Cerastoderma edule* from the Burry Inlet (South Wales) *Palaeontology* 15: 61–72. The Burry Inlet cockles are smaller than those from other British cockle beds and this is due to the longer periods of time at the Burry Inlet when the sands are left exposed by the tide and feeding is reduced.
- FISCHER-PIETTE, E., GAILLARD, J. M. and JAMES, B. L., 1964. Étude sur les variations de *Littorina saxatilis* VI. Quelques cas qui posent de difficiles problèmes. *Cah. Biol. mar.* 5: 125–171. Includes reference to work on populations of winkles from Gower.
- FOWELL, R. R., 1939. Living communities harboured by the oar-weeds (*Laminaria*). *Proc. Swansea scient. Fld. Nat. Soc.* 2: 92–103. *Patina pellucida*, *Lacuna vincta*, *Mytilus edulis* and *Hiattella arctica* were found associated with oar-weed at Langland Bay.
- , 1944. The ecology of a rock pool. *Proc. Swansea scient. Fld. Nat. Soc.* 2: 191–212. Nine species of molluscs are recorded from rock pools and rocks at Langland Bay, Gower. *Lepidochitona cinereus*, *Patella vulgata*, *Gibbula umbilicalis*, *Littorina littorea*, *L. littoralis* agg., *Cingula semistriata*, *Nucella lapillus*, *Modiolus phaseolinus* and *Hiattella arctica*.
- , 1947. An ecological study of an *Enteromorpha* pool. *Proc. Swansea scient. Fld. Nat. Soc.* 2: 306–310. *Littorina saxatilis* agg. and *L. littorea* are recorded from Langland Bay, Gower.
- FRANKLIN, A. and PICKETT, G., 1975. The distribution of the introduced gastropods *Urosalpinx cinerea* and *Crepidula fornicata* in England and Wales. *Conchologists' Newsletter* 55: 462–463. Records *Crepidula fornicata* from Swansea Bay.
- FREYTAG, J., 1977. *Survey of the marine fauna and flora of the Gower coast National Nature Reserve*. University College of Swansea. A compilation of existing knowledge of the marine life (including the marine Mollusca) of south-west Gower from Oxwich Bay to Whitford Point, north of Rhossili. Whilst extensive lists of species were available for Oxwich Bay and Rhossili, less information was available on the exposed rocky shore between Port Eynon and Tears Point. 174 species of marine molluscs are listed with an indication of locality: 101 species are live records.



Quantitative data on the distribution of some species are given as a result of transects worked across the shore at 9 stations.

- GAIN, W. A., 1897. Conchological notes from South Wales. *Naturalists' J.* **6** (62): 105–109. An account of molluscs collected at Langland Bay and Caswell Bay (Gower) and in Swansea Bay near Jersey Marine Station and Mumbles Road Station in 1896.
- GRATTON, P., 1969. Colour polymorphism in *Littorina mariae*. *Bios*, **3**: 53–57. *Littorina mariae* was collected from several stations on Gower.
- HANCOCK, D. A., 1967. Growth and mesh selection in the edible cockle (*Cardium edule* L.). *J. appl. Ecol.* **4**: 137–157. This paper refers to the cockle beds at Llanrhidian Sands, Gower and there is an illustration of a cockle woman raking for cockles.
- and FRANKLIN, A., 1972. Seasonal changes in the condition of the edible cockle (*Cardium edule* L.). *J. appl. Ecol.* **9**: 567–579. An account of research work on the breeding cycles, the quantity of cockle meat and the effect of season on these during the period 1958–60 and 1968–69.
- and URQUHART, A. E. 1964. Mortalities of edible cockles (*Cardium edule* L.) during the severe winter of 1962–63. *J. Anim. Ecol.* **33**: 176–178. Reports on a high mortality of cockles at the Burry Inlet.
- and ———, 1966. The fishery for cockles (*Cardium edule* L.) in the Burry Inlet, South Wales. *Fishery Invest., Lond.* Ser 2, **25** (3): 1–32. A detailed account of the Burry Inlet cockle fishery which provided one third of Britain's cockle harvest in the early 1950's. This cockle fishery has been in existence for over a hundred years.
- HEPPER, H. T., 1957. Notes on *Mytilus galloprovincialis* Lamarck in Great Britain. *J. mar. biol. Ass. U.K.* **36**: 33–40. Records of mixed populations of *Mytilus edulis* and *M. galloprovincialis* at the Mumbles, near Swansea.
- HORWOOD, J. W. and GOSS-CUSTARD, J. D., 1977. Predation by the oystercatcher, *Haematopus ostralegus* (L.), in relation to the cockle, *Cerastoderma edule* (L.), fishery in the Burry Inlet, South Wales. *J. appl. Ecol.* **14**: 139–158. The data for 1958–1972 are examined using a mathematical model. It was shown that, when the cockles fall below a certain level of density the oystercatchers turn to other food. The sizes at which cockles are taken by both birds and fishermen were also studied.
- HOWELLS, W. R., 1952. *The ecology of the estuaries of certain Welsh rivers*. Ph.D. thesis. University College of Wales, Aberystwyth. Includes results of transects worked on the Pembrey Sands and at Llanelli.
- , 1964. The macrofauna of the inter-tidal soils of the Towy Estuary, Carmarthenshire. *Ann. mag. Nat. Hist.* Ser. 13, **7**: 577–607. Includes the results from samples taken in the Burry Estuary and at Llanelli.
- IRELAND, M. P. and WOOTTON, R. J., 1977. Distribution of lead, zinc, copper and manganese in the marine gastropods, *Thais lapillus* and *Littorina littorea* around the coast of Wales. *Environ. Pollut.* **12**: 27–41. The heavy metal content of the bodies and shells of the molluscs were analysed from samples taken at Oxwich, Gower.
- JAMES, B. L., 1968. The characters and distribution of the subspecies and varieties of *Littorina saxatilis* (Olivi 1792) in Britain. *Cah. Biol. mar.* **9**: 143–165. Some specimens used in this study were collected from Gower. The subspecies are illustrated by photographs.
- JENKINS, J. G., 1976. Making a living from shellfish. *Country Life* **154**: 558–559. An illustrated account of the cockle fishery in the Burry Inlet.
- KING, P. E., and OSBORN, A., 1969. Oyster dredging. *Gower* **20**: 76–81. Describes oyster beds along the coast of South Wales including those in Swansea Bay and between Mumbles Head and Port Eynon. The article describes the methods used for dredging and gives illustrations of oyster skiffs and dredges.
- LLOYD, R. J. H., 1954. The Mumbles oyster skiffs. *Mariner's Mirror* **40**: 258–269. Details of the boats which were used for oyster dredging at the Mumbles.
- MATHESON, C., 1934. The oyster fishery at Mumbles. *Trans. Cardiff Nat. Soc.* **66**: 81–86. An account of the Mumbles oyster fishery which operated over several centuries, reaching its peak in the mid-nineteenth century. Towards the end of the nineteenth century there was a decline in production and the last of the oyster skiffs disappeared in 1930.
- McMILLAN, N. F., 1944. The distribution of *Monodonta* (*Trochus*) *lineata* (da Costa) in Britain. *N. West. Nat.* **19**: 290–292. *Monodonta lineata* was recorded by Davy Dean as being abundant in Gower.
- MOYSE, J. and NELSON-SMITH, A., 1964. Effects of the severe cold of 1962–63 upon shore animals in South Wales. *J. Anim. Ecol.* **33**: 183–190. The effects of the hard winter were reported for 24 species of marine mollusc. *Monodonta lineata* was heavily affected with 75% mortality in Swansea Bay and *Patella vulgata* was also affected, especially those specimens living high on the shore.
- NAYLOR, E., 1965. Biological effects of a heated effluent in docks at Swansea, S. Wales. *Proc. zool. Soc. Lond.*, **144**: 253–268. *Mytilus edulis* and *Teredo navalis* L. were recorded from Queen's Dock, Swansea during 1956–1958.
- , 1971. Zoology. From 'Swansea and its region' Edited by BALCHIN, W. S. V. for the British Association. University College of Swansea, Swansea. pp. 101–118. A general account of the marine fauna of Gower with distribution records of some of the marine molluscs. There is reference to *Littorina mariae* which was formerly included in the aggregate species *Littorina littoralis* (Flat wrinkle). The effects of crude oil and detergents on the molluscs are considered.
- NICKLESS, G., STENNER, R. and TERRILLE, N., 1972. Distribution of cadmium, lead and zinc in the Bristol Channel. *Mar. Pollut. Bull.* **3**: 188–190. Records the heavy metal levels in *Patella*, *Nucella*, *Littorina* and *Mytilus* at Oystermouth, Mumbles, Bracelet Bay and Rhossili. A secondary source of pollution was reported in the Swansea area.



- PAIN, C., 1978. Report of the field meeting held at Rhosilli, Gower, 6–7 May, 1978. *Conchologists' Newsletter*, **66**: 100.
- PASCOE, D., 1968. *Studies on the metabolism of Digenea from sea birds and molluscs*. Ph.D. Thesis, University College of Swansea, University of Wales. *Cerastoderma edule* used in this study were collected from Llanrhidian Sands (1967–1968).
- PEARCE, D. W., 1967. *Studies on the plankton of the Bristol Channel*. M.Sc. Thesis. University College of Swansea. This includes plankton hauls collected at the Mumbles and Swansea Docks. Although the total numbers of veligers are given, they were not identified beyond class level. *Mytilus edulis* was recorded settling in the dock.
- PURCHON, R. D., 1957. Studies on the biology of the Bristol Channel XVIII. The marine fauna at five stations on the northern shores of the Bristol Channel and Severn Estuary. *Proc. Bristol Nat. Soc.* **29**: 213–226. Includes a short section on the sublittoral fauna of Swansea Bay, with a report on the condition of the oyster beds.
- QUICK, H. E., 1949. *Limapontia depressa* Alder and Hancock in Suffolk and Glamorgan. *J. Conch., Lond.*, **23**: 84. Records the sacoglossan *Limapontia depressa* from a salt-marsh near Penclawdd, Gower.
- , 1950. Observations on *Limapontia*. *Proc. malac. Soc. Lond.*, **28**: 134–138. Further details on *Limapontia depressa* on the Lougher Estuary between Gowerton and Penclawdd. Other molluscs recorded with them were *Hydrobia ulvae* and *Ovatella myosotis* (Draparnaud).
- TAYLOR, D. L., 1967. *Symbiotic relationships between some marine plants and animals*. Ph.D. Thesis. University College of Swansea, University of Wales. Specimens of *Hermaea dendritica* (Alder and Hancock) were collected from Port Eynon, Gower.
- WARWICK, R. M., and DAVIES, J. R., 1977. The distribution of sublittoral macrofauna communities in the Bristol Channel in relation to substrate. *Est. coast. mar. Sci.* **5**: 267–288. Records the common species of marine mollusc from a number of grab samples taken off-shore from this section of the Welsh coast. It includes many live records of species whose shells are commonly washed up on Gower beaches.
- WITHERS, R. G., 1968. Locomotor activity in *Patella vulgata*. *Bios.* **2**: 43–46. The limpets used in the experiments were collected from Mumbles Head, Swansea.
- , 1972. *Aspects of the ecology of marine sand-dwelling macrobenthos*. Ph.D. Thesis. University College of Swansea, University of Wales. This includes a description of the physical features of Oxwich Bay and records of molluscs and other animals found along three transect lines. Nine species of gastropods and 18 species of bivalves were recorded together with information on distribution, population densities, growth rate and life cycles. The grade of sediment was shown to affect the species of molluscs present.
- YONGE, C. M., 1959. On the structure, biology and systematic position of *Pharus legumen* (L.). *J. mar. biol. Ass. U.K.* **38**: 277–290. The source of some of the specimens used was Oxwich Bay (collected by Professor Knight-Jones). *Pharus legumen* was reported as being more common at Oxwich than it was on Anglesey.

CARMARTHEN BAY, LLANELLI TO MANORBIER. (County of Dyfed) Marine Census Area 21.

- ADAMS, J., 1800. Descriptions of some minute British shells. *Trans. Linn. Soc. Lond.* **5**: 1–6. Records of shells found in shell sand at Tenby.
- ANON., 1894. Proceedings of the Conchological Society—Exhibits. *J. Conch., Lond.* **7**: 360. *Glossus humanus* (L.) and *Colus islandicus* (Gmelin) from Carmarthen Bay, exhibited by Mr. R. D. Darbishire.
- BARKER, T. W., 1905. *Handbook to the Natural History of Carmarthenshire*. Spurrell, Carmarthen. Includes a list of 79 species, mostly from Pendine. The list was compiled as a result of collecting by the author and by inclusion of further information from Mr. Bartlet Span.
- COWELL, E. B. and CROTHERS, J. H., 1970. On the occurrence of multiple rows of 'teeth' in the dog-whelk *Nucella lapillus* (L.). *J. mar. biol. Ass. U.K.* **50**: 1101–1111. A list of localities from which *Nucella lapillus* was collected.
- CROTHERS, J. H., 1971. Further observations on the occurrence of 'teeth' in the dog-whelk *Nucella lapillus*. *J. mar. biol. Ass. U.K.* **51**: 623–639. Records *Nucella lapillus* from Marros Sands.
- , 1974. On variation in the shell of the dog-whelk *Nucella lapillus* (L.). in Pembrokeshire. *Fld. Stud.* **4**: 39–60. Refers to *Nucella lapillus* at Tenby.
- , 1974. On variation in *Nucella lapillus* (L.): shell shape in populations from the Bristol Channel. *Proc. malac. Soc. Lond.* **41**: 157–170. Records *Nucella lapillus* from Marros Sands, Amroth, Tenby and Lydstep.
- CUNDALL, J. W., 1889. A list of shells taken at Tenby, September, 1888. *J. Conch., Lond.* **6**: 102–106. An account of shore collecting at Tenby, Lydstep, Giltar Point and Saundersfoot, with notes on the abundance of the individual species. Eighty-four species of marine molluscs are recorded.
- , 1890. Tenby Shells. *J. Conch., Lond.* **6**: 250. A note adding *Retusa truncatula* (Bruguère) and *Alvania crassa* (Kanmacher) to the list of Tenby shells.
- DONOVAN, E., 1805. *Descriptive excursions through South Wales and Monmouthshire in the year 1804 and the four preceding summers*. F. and C. Rivington, London 2 vols. Refers to shells on the beach at Pendine and Tenby and to oyster beds at Caldy Island.
- EVANS, R. G., 1949. The intertidal ecology of rocky shores in South Pembrokeshire. *J. Ecol.*, **37**: 120–139. A description of the coast and marine life in the Tenby area (Manorbier to Telpyn Point). The account of the marine molluscs is general rather than specific and only 19 species are mentioned. The description of the shore and habitats is quite detailed.



## CHATFIELD: MARINE MOLLUSCS IN WALES

- FRETTER, V. and GRAHAM, A., 1954. Observations on the opisthobranch mollusc *Acteon tornatilis* (L.). *J. mar. biol. Ass. U.K.* **33**: 565–585. Describes a living population of *Acteon tornatilis* at Pendine with observations on the living animals and on the anatomy.
- GARDINER, A. P., 1945. British marine records. *J. Conch., Lond.* **22**: 148. *Cirsotrema commutatum* (Monterosato) and *Mytilus galloprovincialis* at Pendine and *Nucella lapillus* with reduced opercula at Lydstep.
- GOSSE, P. H., 1856. *Tenby: a seaside holiday*. Van Voorst, London. Seven species of marine molluscs are recorded for Tenby and others from Lydstep, Caldy Island, and Amroth.
- GREEN, J., 1957. The growth of *Scrobicularia plana* (Da Costa) in the Gwendraeth Estuary. *J. mar. biol. Ass. U.K.* **36**: 41–47. Reports on a population of large specimens of *Scrobicularia plana* at densities up to 1025/metre<sup>2</sup> in mud at the eastern end of Carmarthen Bay.
- HEPPER, H. T., 1957. Notes on *Mytilus galloprovincialis* Lamarck in Great Britain. *J. mar. biol. Ass. U.K.* **36**: 33–40. Records mixed populations of *Mytilus edulis* and *Mytilus galloprovincialis* at Pendine and Tenby.
- HOWELLS, W. R., 1964. The macrofauna of the intertidal soils of the Towy Estuary, Carmarthenshire. *Ann. Mag. Nat. Hist.* Ser 13, **7**: 577–603. Results of transects worked on the east shore of the estuary from Ferryside to Carmarthen. Some additional samples were taken at Llanelli and at Pembrey. The marine molluscs recorded were: *Hydrobia ulvae*, *Macoma balthica*, *Scrobicularia plana*, *Tellina tenuis*, *Donax vittatus* and *Cerastoderma edule*.
- IRELAND, M. P. and WOOTTON, R. J., 1977. Distribution of lead, zinc, copper and manganese in the marine gastropods, *Thais lapillus* and *Littorina littorea* around the coast of Wales. *Environ. Pollut.* **12**: 27–41. The heavy metal content of the molluscs was analysed for a sample collected from Tenby.
- LEWES, G. H., 1858. *Sea-side studies at Ilfracombe, Tenby, the Scilly Isles and Jersey*. Blackwood, London. An account of collecting activities and general information rather than a contribution to the distribution of marine molluscs of the Tenby area.
- MASON, R., 1866. *Guide to Tenby and its neighbourhood*. Mason, Tenby. Includes a section on conchology in which 64 of the less common species are listed. The author considered that dredging was necessary to form a good collection. Beaches good for shore collecting included South Sands, Tenby, Waterwinch and Saundersfoot.
- MILNES, H., 1883. A conchological ramble at Tenby. *Sci. gossip* **19**: 174–175. Twelve species of marine molluscs are recorded with notes on the habitats.
- MOYSE, J. and NELSON-SMITH, A., 1964. Effects of the severe cold of 1962–63 upon shore animals in South Wales. *J. Anim. Ecol.* **33**: 183–190. Records the effect of the cold winter on a number of marine molluscs. More than 75% mortality was recorded for *Monodonta lineata* in Carmarthen Bay.
- NICKLESS, G., STENNER, R. and TERRILLE, N., 1972. Distribution of cadmium, lead and zinc in the Bristol Channel. *Mar. pollut. Bull.* **3**: 188–190. Records the levels of heavy metals in *Patella*, *Littorina*, *Nucella* and *Mytilus* at Laugharne, Pendine, Amroth, Saundersfoot, Tenby and Lydstep Haven. A sharp drop in heavy metals in mollusc tissue was noted at, and westward of, Carmarthen Bay.
- OLDHAM, C., 1930. The shell-smashing habit of gulls. *Ibis*, Ser. 12, **6**: 239–243. Herring gulls at Tenby were reported dropping shells of *Buccinum undatum* (occupied by hermit crabs) onto sand and rocks.
- PURCHON, R. D., 1957. Studies on the biology of the Bristol Channel. XVIII. The marine fauna at five stations on the northern shores of the Bristol Channel and Severn Estuary. *Proc. Bristol. Nat. Soc.* **29**: 213–226. Includes a short description of the shore at Marros with a list of marine molluscs found there.
- ROBERTS, T., 1976. *Detailed guide to the beaches of Pembrokeshire, Cardiganshire and Carmarthenshire*. Abercastle Publications, Abercastle, Dyfed. A useful description of many beaches in this region with information on access.
- SPAN, B., 1899. A contribution towards a list of the marine Mollusca of Tenby and neighbourhood. *J. Conch., Lond.* **9**: 203–211. The most extensive list of marine shells published for the Tenby district (Laugharne to Milford Haven) comprising some 178 species and additional varieties. There are useful additional notes on the individual species. Compiled from shore collecting and dredging over a period of ten years.
- TYE, G. S., 1874. List of shells taken at Tenby, Pembrokeshire, at the end of September 1872. *J. Conch., Lond.* **1**: 30–31. Sixteen species of marine molluscs are listed together with some habitat notes. This included results of dredging.
- WARWICK, R. M. and DAVIES, J. R., 1977. The distribution of sublittoral macrofauna communities in the Bristol Channel in relation to substrate. *Est. coast. mar. Sci.* **5**: 267–288. A report of off-shore grab samples in Carmarthen Bay and mid-channel from Caldy Island, eastward in 1972–1973. Common marine molluscs are recorded and these are the species which are commonly washed up on the beaches in this area.
- WILLIAMS VAUGHAN, J., 1905. The marine Mollusca of Tenby and neighbourhood: a further contribution. *J. Conch., Lond.* **11**: 216–218. An annotated list of additions to Span's list of shells for Tenby (Span 1899).
- WITHERS, R. G., 1977. Soft-shore Macrobenthos along the south-west coast of Wales. *Est. coast. mar. Sci.* **5**: 467–484. Results of transects worked across the shore at Tenby, Saundersfoot and Pendine. Marine molluscs were recorded on all of these transects.

### THE PEMBROKESHIRE COAST. (County of Dyfed) Marine Census Area 21.

- ADDY, J. M., 1976. Preliminary investigations of the sublittoral macrofauna of Milford Haven. In: BAKER, J. M. (Ed.), *Marine ecology and oil pollution*. Applied Science Publishers Ltd. Barking, Essex. pp. 91–130. An account of the marine Mollusca from soft sub-littoral deposits in Milford Haven collected in 26 grab samples (1974). Sixteen



- species of bivalves and 3 species of gastropods are recorded. The results show the distribution of these species in Milford Haven.
- ARNOLD, D. C., 1972. Salinity tolerances of some common prosobranchs. *J. mar. biol. Ass. U.K.*, **52**: 475–486. Maps of distribution are given for species of *Patella*, *Gibbula*, *Nucella* and *Littorina* in Milford Haven where rocky shores occur higher up the estuary than in most other estuary systems.
- BAILEY, J. H., NELSON-SMITH, A. and KNIGHT-JONES, E. W., 1967. Some methods for transects across steep rocks and channels. *Underwat. Ass. Rep.* (1966–1967): 107–111. Although primarily concerned with the methods for underwater transects, some results are given showing the distribution of animals (including a few species of molluscs) along a transect line across Milford Haven. A large population of *Crepidula fornicata* was noted.
- BAKER, J. M. (Ed.), 1976. *Marine ecology and oil pollution*. Applied Science Publishers, Barking, Essex. Chapters 6 and 11 (by J. M. Baker) refer to the effect of oil pollution on marine molluscs.
- BALLANTINE, W. J., 1961. A biologically-defined exposure scale for the comparative description of rocky shores. *Fld. Stud.* **1**: (3), 1–19. A comparative study of the flora and fauna of rocky shores of varying exposures on the Dale peninsula. It includes records of 10 species of common rocky shore molluscs from 28 stations.
- BASSINDALE, R., 1946. Studies on the biology of the Bristol Channel XVI. The fauna of Skomer Island. A preliminary sketch. *Proc. Bristol Nat. Soc.* **27**: 109–120. A faunal list of the marine life of Skomer which provides a good range of rocky shores. Twenty-eight different marine molluscs are listed, but some are named to genus level only.
- , 1950. Marine list of Skomer pp. 148–153. In: BUXTON, J. and LOCKLEY, R. (Ed.). Staples Press, London. Most of the recording concerns intertidal species of which 30 are listed. The two dredging excursions yielded 6 species of live molluscs and the empty shells of 4 others. Field work was under-taken in both North and South Havens.
- , 1958. Marine biology. In: Island of Skomer. A special supplement. *Nature Wales* **4**: 690–694. Only a very general account of the marine molluscan fauna, but including mention of Key-hole Limpets and Slit Limpets.
- and BARRETT, J. H., 1957. The Dale Fort marine fauna. *Proc. Bristol. Nat. Soc.* **29**: 227–328. An annotated faunal list (with localities, dates of collection, names of collectors and other notes) for the Dale Fort area which includes 156 species of marine molluscs.
- and CLARK, R. B., 1960. The Gann Flat, Dale: studies on the ecology of a muddy beach. *Fld. Stud.* **1** (2): 1–22. An account of the physical environment and general nature of the fauna. Twenty-one species of gastropods and 30 species of bivalves are recorded.
- BERRY, R. J. and CROTHERS, J. H., 1968. Stabilizing selection in the dog-whelk, *Nucella lapillus*. *J. Zool., Lond.* **155**: 5–17. Gives a list of collecting sites in Pembrokeshire.
- and ———, 1974. Visible variation in the dog-whelk, *Nucella lapillus*. *J. Zool., Lond.* **174**: 123–148. Gives lists of collecting sites for *Nucella lapillus* all around the Welsh coast.
- COLE, H. A. and BAIRD, R. H., 1953. The American slipper limpet *Crepidula fornicata* in Milford Haven. *Nature* **172**: 687. Records 6 slipper limpets found near Pennar Gut on the estuary of the Pembroke River.
- COUGHLAN, J., 1969. *Milford Haven: A preliminary species list for the Pwllcrochan shore*. Central Electricity Generating Board Laboratory note no. RD LN 2769. A survey of the species of marine animals and their habitats from the Pwllcrochan shore undertaken from 1966–1968. Forty-one species of marine Mollusca are listed which include rocky shore species and also some species which occur in soft substrata.
- COWELL, E. B., (Ed.) 1971. *The ecological effects of oil pollution on littoral communities*. The Institute of Petroleum, London. Applied Science Publishers Ltd., Barking, Essex. A series of papers by different authors concerning the effects of oil pollution and subsequent cleansing on the flora and fauna of shores of Milford Haven. There are a number of references to marine molluscs.
- and CROTHERS, J. H., 1970. On the occurrence of multiple rows of 'teeth' in the dog-whelk *Nucella lapillus* (L.). *J. mar. biol. Ass. U.K.* **50**: 1101–1111. A list of localities is given from which *Nucella lapillus* was collected: these are mostly in Pembrokeshire. The date of collection is also included.
- CRAPP, G. B., 1966. Oil pollution in Milford Haven. *Nature Wales* **11**: 131–137. This paper concerns the problem of oil pollution and there is nothing specifically on molluscs.
- , 1970. *The biological effects of marine oil pollution and shore cleansing*. Ph.D. Thesis. University College of Swansea, University of Wales. Twenty two transect sites were used to monitor the marine life of rocky shores and 9 species of molluscs were recorded (using an abundance scale). There was no evidence to suggest that the fauna had deteriorated following the establishment of the Milford Haven oil terminal. The marine life was also investigated on sandy and muddy shores at West Angle Bay (no molluscs), Mun Sands (4 species), Kilpaison (3 species) and West Llanion Pill (3 species). Raw data are given in the Appendix.
- , WITHERS, R. G., and SULLIVAN, C. E., 1971. Investigations on Sandy and Muddy Shores. In: COWELL, E. B., (Ed.) *The Ecological Effects of Oil Pollution on Littoral Communities*. Institute of Petroleum. Applied Sciences Publishers Ltd. Barking, Essex. Results of transects across some beaches in Milford Haven. Three species of bivalves were recorded on some of the transects.
- CREMER, G. A., FARRER, M. E. and STACHES, B. W., 1965. The distributions of dominant animals in relation to exposure on Skokholm shores. *Rep. Skokholm Bird Obs.* (1965); 25–31. Results of 10 transects worked in the autumn of 1964 around the island. Thirteen species of gastropods and 4 species of bivalve are recorded, together with an indication of abundance and notes on the individual species.
- CROTHERS, J. H., 1966. Dale Fort marine fauna. 2nd edition. *Fld. Stud.* supplement to Volume 2: 169 pp. Lists 314



species of marine molluscs with notes on habitats and localities: the list is in systematic order. The most complete account of the molluscan fauna for this stretch of coast.

- , 1971. Further observations on the occurrence of 'teeth' in the dog-whelk *Nucella lapillus*. *J. mar. biol. Ass. U.K.* **51**: 623–639. A detailed list of localities and dates of collection (1969–70) of *Nucella lapillus* including some in Pembrokeshire.
- , 1973. On variation in *Nucella lapillus* (L.): shell shape in populations from Pembrokeshire, South Wales. *Proc. malac. Soc. Lond.* **40**: 319–327. Includes a list of localities with grid references and date of collection.
- , 1974a. On variation in the shell of the dog-whelk, *Nucella lapillus* (L.). Pembrokeshire. *Fld. Stud.* **4**: 39–60. Includes a list of localities with grid reference and date of collection.
- , 1974b. On variation in *Nucella lapillus* (L.): shell shape in populations from the Bristol Channel. *Proc. malac. Soc. Lond.* **41**: 157–170. Records *Nucella lapillus* for nine localities on the shores of Milford Haven and the Angle peninsula.
- DIAS, N. S., 1960. *Studies on the plankton of Milford Haven*. M.Sc. Thesis, University of Wales. This does not include very much detailed information on molluscs since the mollusc veligers were not identified with the exception of *Cultellus pellucidus*, *Hiatella arctica*, and *Anomia* spp. *Littorina littorea* was recorded from egg capsules and 2 specimens of *Sepioloatlantica* Orbigny were taken on a night haul in the mouth of the Haven. The numbers of veliger larvae are given in the data chart.
- DOBSON, M., EVANS, F. and JAMES, K., 1971. The sediments on the floor of the southern Irish Sea. *Marine Geology* **11**: 27–69. This includes results from samples of shelly bottom material dredged in the middle of the Irish Sea on a level with St Davids and Cardigan. The list of species is given in the appendix.
- DONOVAN, E., 1805. *Descriptive excursions through South Wales and Monmouthshire, in the year 1804 and the four preceding summers*. 2 vols. Rivington, London. Mention of *Acanthochitona crinitus* (Pennant) at Milford Haven.
- FALLOON, B. J., 1890. *Otina otis* var. *candida* in Pembrokeshire. *J. Conch., Lond.* **6**: 264. *Otina ovata* (Brown), a small marine pulmonate is recorded from caves Eligug Stack Rocks.
- FISCHER-PIETTE, E., GAILLARD, J.-M. and JAMES, B. L., 1964. Étude sur les variations de *Littorina saxatilis* VI. Quelques cas qui posent de difficiles problèmes. *Cah. Biol. mar.* **5**, 125–171. Includes work on collections of winkles from Pembrokeshire.
- FRANKLIN, A. and PICKETT, G., 1975. The distribution of the introduced gastropods *Urosalpinx cinerea* and *Crepidula fornicata* in England and Wales. *Conchologists' Newsletter* **55**: 462–463. Records *Crepidula fornicata* in Milford Haven.
- GARDINER, A. P., 1945. British marine records. *J. Conch., Lond.* **22**: 148. Records *Acanthochitona discrepens* (Brown) at Neyland, Milford Haven 1945. *Calliostoma zizyphinum conuloide* was reported as being wiped out in Milford Haven as a result of oil pollution.
- GEORGE, M., 1961. Oil pollution of Marine Organisms. *Nature* **192**: 1209. Observations on marine life following some oil spills in Milford Haven. The emulsifiers used to clean the shores proved more toxic to the limpets than did the oil. The rasping action of limpets feeding on the surface of the rocks did help to remove some of the hardened oil.
- GRATTON, P., 1969. Colour polymorphism in *Littorina mariae*. *Bios.* **3**: 53–57. *Littorina mariae* was collected from 10 named localities on Milford Haven.
- HELLER, J., 1975a. The taxonomy of some British *Littorina* species with notes on their reproduction (Mollusca: Prosobranchia). *Zool. J. Linn. Soc.* **56**: 131–151. This paper examines the species complex *Littorina saxatilis* agg. and divides it into four species: *L. rudis* Maton, *L. patula* Jeffreys, *L. nigrolineata* Gray and *L. neglecta* Bean. The differences between the species are outlined and there is a list of Pembrokeshire localities. A key paper for the *L. saxatilis* problem.
- , 1975b. Visual selection of shell colour in two littoral prosobranchs. *Zool. J. Linn. Soc.* **56**: 153–170. Substantial lists of localities are given for *Littorina rudis* and *L. nigrolineata* in Pembrokeshire. The paper discusses variation in shell colour within the species.
- , 1976. The effects of exposure and predation on the shell of two British winkles. *J. Zool., Lond.*, **179**: 201–213. The shell shapes of *Littorina nigrolineata* and *L. rudis* were compared for exposed and sheltered shores. Field-work was undertaken on the Dale peninsula.
- HEPPER, H. T., 1956. The European flat oyster, *Ostrea edulis* L. as a host for *Mytilicola intestinalis* Steur. *J. Anim. Ecol.* **25**: 144–147. The sample of 60 oysters collected from Milford Haven (which had been relaid from oysters from the Menai Straits) did not show any infection with the copepod *Mytilicola intestinalis* whilst 85–100% of the mussels (*Mytilus edulis*) taken from Milford Haven were infected with the parasite.
- , 1957. Notes on *Mytilus galloprovincialis* Lamarck in Great Britain. *J. mar. biol. Ass. U.K.* **36**: 33–40. Mixed populations of *Mytilus edulis* and *M. galloprovincialis* were recorded at Angle Bay.
- HUNHAM, P. and BROWN, G., 1975. Sublittoral nudibranch Mollusca (sea-slugs) in Pembrokeshire waters. *Fld. Stud.* **4**: 131–159. A detailed account of the sea-slugs found around the Dale peninsula and Skomer Island with descriptions and illustrations of the species and some records new to Wales. Forty-two species are listed.
- JAMES, B. L., 1968a. The characters and distribution of the sub-species and varieties of *Littorina saxatilis* (Olivi 1792) in Britain. *Cah. Biol. mar.* **9**: 143–165. *Littorina saxatilis* agg. were collected from the Dale area, Skomer and St. Govan's. The sub-species are illustrated by photographs.
- , 1968b. The distribution and keys of species in the family Littorinidae and of their digenean parasites, in the region of Dale. *Fld. Stud.* **2**: 615–650. The paper includes information on the identification of both winkles and of their



- digenean parasites including a good list of references to the parasites in the molluscs. Parasites were recorded from *Littorina littorea*, *L. neritoides* (at Skomer Head) and from four of the species of *L. saxatilis* agg. No parasites were recorded from *L. obtusata* or *L. mariae* (= *L. littoralis* agg.) in this study.
- JAMES, M., 1973. *Ultrastructure and histochemical studies on larval Digenea from marine molluscs*. Ph.D. Thesis. University College of Swansea, University of Wales. *Gibbula umbilicalis* was collected from Sandy Haven (north shore of Milford Haven) and West Angle Bay.
- JARMAN, R. T. and de TURVILLE, C. M., 1977. *Symposium on Pembroke Power Station and Milford Haven*. Central Electricity Generating Board. South Western Board. A report of the symposium with summaries of the papers. Only one paper includes reference to molluscs.
- LEMICHE, H. and THOMPSON, T. E., 1974. Three opisthobranch gastropods new to the British fauna. *Proc. malac. Soc. Lond.* **41**: 185–193. Records *Polycera faeroensis* from the vicinity of Dale and describes a new species, *Favorinus blianus* from Martinshaven, Pembrokeshire.
- McMILLAN, N. F., 1944. The distribution of *Monodonta* (*Trochus*) *lineata* (da Costa) in Britain. *NWest Nat.* **19**: 290–292. Refers to *Monodonta lineata* in Pembrokeshire.
- MOYSE, J., 1958. Patterns of intertidal distribution around Dale. *Rep. Fld. Stud. Counc.* 1956–7: 43–51. A general account of the coastline around Dale and the zonation of species on the shore. It includes records of the four classic species of *Littorina*, *Patella vulgata*, *P. aspera*, *Nucella lapillus*, *Gibbula umbilicalis* and *Mytilus edulis*.
- and NELSON-SMITH, A., 1963. Zonation of animals and plants on rocky shores around Dale, Pembrokeshire. *Fld. Stud.* **1**: (5), 1–31. Results of transects worked across rocky shores on the Dale peninsula. The histograms produced show the extent of distribution in the tidal zones of the *Littorina* species, *Monodonta lineata*, *Gibbula umbilicalis*, *G. cineraria*, 3 species of *Patella* and *Nucella lapillus*.
- and —, 1964. Effects of the severe cold of 1962–63 upon shore animals in South Wales. *J. Anim. Ecol.* **33**: 183–190. Records abundance and mortality rate of *Monodonta lineata* with notes on the effect of the cold on some other species of marine molluscs in Pembrokeshire.
- NELSON-SMITH, A., 1964. *Some aspects of the marine ecology of Milford Haven, Pembrokeshire*. Ph.D. Thesis, University College of Swansea. This includes a description of the habitats and a short account of the effect of oil pollution on marine life with reference to named species of molluscs. The distribution in Milford Haven of several species of marine molluscs was investigated on the shore. Under-water sub-littoral transects resulted in the recording of 5 species of gastropods and 5 species of bivalves. The factors limiting the distribution of common marine species in the Haven are discussed.
- , 1967. Marine biology of Milford Haven: the distribution of littoral plants and animals. *Fld. Stud.* **2**: 435–477. Includes the distribution of *Patella vulgata*, *P. aspera*, *P. depressa*, *Monodonta lineata*, *Gibbula umbilicalis*, *G. cineraria*, *Calliostoma zizyphinum*, *Littorina neritoides*, *L. saxatilis* agg. *L. littoralis* agg., *L. littorea* and *Nucella lapillus* with reference also to *Ocenebra erinacea*, *Crepidula fornicata* and *Mytilus edulis*.
- , 1968. The effects of oil pollution and emulsifier cleansing on marine life in south west Britain. *J. appl. Ecol.* **5**: 97–107. The paper gives a brief history of oil pollution in south west Britain and comments on the effects of both oil and emulsifiers on some marine molluscs. It includes some results of transect work at two sites on Milford Haven before and after pollution and spraying.
- , 1970. The problem of oil pollution of the sea. *Adv. mar. Biol.* **8**: 215–306. A general account of the oil pollution problem but with some references to the effects on marine molluscs and examples from Milford Haven.
- NICKLESS, G., STENNER, R. and TERRILLE, N., 1972. Distribution of cadmium, lead and zinc in the Bristol Channel. *Mar. Pollut. Bull.* **3** (12): 188–190. Reports on the levels of some heavy metals in the tissue of some common marine molluscs with samples from Freshwater West, Dale Roads, and Westdale Bay.
- PEARCE, D. W., 1967. *Studies on the plankton of the Bristol Channel*. M.Sc. Thesis. University College of Swansea. This includes some plankton hauls collected off Pembrokeshire. Although the total numbers of veligers are given, they were not identified beyond class level.
- ROBERTS, T., 1976. *Detailed guide to the beaches of Pembrokeshire, Cardiganshire and Carmarthenshire*. Abercastle Publications, Abercastle, Dyfed. A useful description of many beaches in this region with information on access.
- SAWYER, J. T., 1972. Field meeting weekend in Pembrokeshire 21–24 May 1971. *Conchologists' Newsletter* **41**: 256–260. Lists of marine molluscs recorded from The Gann at Dale, St. Brides, Broad Haven, Newgale, Newport and Freshwater Bay.
- SPAN, B., 1899. A contribution towards a list of the marine Mollusca of Tenby and neighbourhood. *J. Conch., Lond.* **9**: 203–211. Records of marine molluscs from St. Govan, Freshwater West, Milford Haven, Newgale Sands and St. Brides Bay.
- STRATTON, L. W., 1964. Collecting at Dale. *J. Conch., Lond.* **25**: 255–263. Records the marine molluscan assemblages found at 15 localities around Dale.
- TAYLOR, D. A. J., 1971. Shelling in Glamorgan and Pembrokeshire and Scilly Isles. *Conchologists' Newsletter* **38**: 234–240. Records marine molluscs from Martin's Haven, Wooltack Point and Pigstone Bay (Skomer Island). Details of the status of the specimen and notes on the abundance are given. A number of the molluscs were collected by diving.
- WALTON, C. L. 1920. A contribution to the ecology of some cockle beds. *Rept. Lancs. Sea-Fish Labs.* **28**: 34–46. Refers to cockles at Pwllcrochan and Langum in Milford Haven.



- WITHERS, R. G., 1972. *Aspects of the ecology of marine sand-dwelling macrobenthos*. Ph.D. Thesis. University College of Swansea, University of Wales. Much of this thesis relating to the Pembrokeshire coast is now published (WITHERS 1977).
- , 1977. Soft-shore Macrobenthos along the South-west Coast of Wales. *Est. coast. mar. Sci.* **5**: 467–484. The marine fauna was investigated along beach transect lines at Lindsay Bay, Mun Sands, Sandy Haven, Kilpaison, Angle Bay, West Angle Bay, Freshwater West, and Freshwater East. No live molluscs were found in the samples from four of these localities.

## CARDIGAN BAY (CARDIGAN TO HARLECH). (Counties of Dyfed and Gwynedd) Marine Census Area 22.

- ANON, 1905. Exhibits. *J. Conch., Lond.* **11**: 219. Specimens of marine shells from Mochras Island near Harlech exhibited by Mr. J. Cosmo Melvill with comments on the productivity of the locality for shells.
- BEANLAND, F. L., 1926. *Results of a quantitative faunal study undertaken in the Dovey estuary, between tide marks applied to the question of marine 'Animal Communities'*. M.Sc. Thesis. University College of Wales, Aberystwyth. The study area was on the south shore of the Dyfi estuary at Ynyslas. For the list of species, see BEANLAND 1940. The raw data charts give numbers of each species found in the samples and there are also figures for the total weights of *Macoma balthica* and *Cerastoderma edule*.
- , 1940. Sand and mud communities in the Dovey estuary. *J. mar. biol. Ass. U.K.* **24**: 589–611. A general ecological study carried out in 1925–6. A typical reduced estuarine fauna of Mollusca was recorded which included *Hydrobia ulvae*, *Retusa obtusa*, *Cerastoderma edule*, *Macoma balthica*, *Tellina tenuis* and *Scrobicularia plana*.
- CHASTER, G. W., 1892. Shell hunting in Merionethshire. *J. Conch., Lond.* **7**: 78–9. Reports that an afternoon spent on the shore was disappointing with *Epilepton clarkiae* as the only noteworthy species. The locality was not given, only the county!
- CHATFIELD, J. E., 1976. Sacoglossans again! *Conchologists' Newsletter* **57**: 502. Records *Limapontia depressa* on a small salt-marsh at Bontddu near Dolgellau on the Mawddach estuary.
- COTTON, J. J., 1930. *Shells found at Mochras and shores of Cardigan Bay*. The Collector's Guide. Jones, Barmouth. 209 species of marine molluscs are listed giving both scientific and common names.
- CROTHERS, J. H., 1971. Further observations on the occurrence of 'teeth' in the dog-whelk *Nucella lapillus*. *J. mar. biol. Ass. U.K.* **51**: 623–639. Includes some localities for *Nucella lapillus*.
- DAVID, H. M., 1941. *The ecology of marked areas on the Aberystwyth shore*. Ph.D. Thesis, University College of Wales, Aberystwyth. Results of a belt transect worked on the rocky shore at Aberystwyth in 1938–1941. Some areas of rock were cleared of existing life and the subsequent colonization studied. Six common species of marine molluscs were recorded.
- DEAN, J. D., 1906. The shell beach at Mochras Island. *J. Conch., Lond.* **11**: 297. J. Davy Dean states his view that Mochras Island is overestimated as a place for shells and that Harlech is a better collecting site. A list of eleven shells from the beach at Harlech is included.
- DESAI, B. N., 1959. *Studies on the biology of the Intertidal Gastropoda*. Ph.D. thesis. University College of North Wales, Bangor. The thesis is mostly on *Monodonta lineata* collected at Criccieth where two transects were worked on the shore.
- , 1966. The biology of *Monodonta lineata* (da Costa). *Proc. malac. Soc. Lond.* **37**: 1–17. Most of the work in this paper (on breeding cycles, growth and zonation) was based on a population of Top Shells at Criccieth.
- DOBSON, M., EVANS, F. and JAMES, K., 1971. The sediments on the floor of the southern Irish Sea. *Marine Geology* **11**: 27–69. This includes data on molluscs from shelly bottom material dredged in the middle of the Irish Sea on a level with Cardigan and Aberystwyth in the south of Cardigan Bay. The list of species is given in the appendix.
- DURLACHER, F. W., 1914. On the drift of sewage in the Dovey estuary in relation to the mussel beds. *Rep. Lancs. Sea-Fish. Labs.* (1913) **22**: 335–344. Includes a map showing the location of mussel beds.
- EVANS, R. G., 1947a. The intertidal ecology of Cardigan Bay. *J. Ecol.* **34**: 273–309. The study area includes the southern part of Borth and the shore up to 1 mile to the south. The shore is bounded by steep cliffs and the beaches below often have more sand than rock on the lower shore. The exposed nature of this coast is reflected in the impoverished fauna. The following species occurred: *Patella vulgata*, *P. depressa*, *P. aspera*, *Patina pellucida*, *Acmaea virginea*, *Monodonta lineata*, *Gibbula umbilicalis*, *G. cineraria*, *Littorina neritoides*, *L. littoralis* agg. *L. saxatilis* agg., *L. littorea*, *Nucella lapillus* and *Mytilus edulis*.
- , 1947b. Studies on the biology of British limpets. Part I. The genus *Patella* in Cardigan Bay. *Proc. zool. Soc. Lond.* **117**: 411–423. The limpet population studied on the coast of Cardigan Bay (between Llangrannog and Borth) consists of three separate species, *P. vulgata*, *P. aspera* and *P. depressa*. Distinguishing features are given for the identification of these three species.
- , 1948. The lethal temperatures of some common British littoral gastropods. *J. Anim. Ecol.* **17**: 165–173. Eleven species of molluscs common on the shores of Cardigan Bay were used in the experiments.
- , 1949. The intertidal ecology of rocky shores in South Pembrokeshire. *J. Ecol.* **37**, 120–139. The paper mostly refers to the Pembrokeshire coast, but the fauna is compared with that of Cardigan Bay.
- FISCHER-PIETTE, E., GAILLARD, J.-M. and JAMES, B. L., 1964. Étude sur les variations de *Littorina saxatilis*. VI Quelques



- cas qui posent de difficiles problèmes. *Cah. Biol. mar.* 5: 125–171. Includes work on collections of winkles from Cardigan Bay.
- FISH, J. D., 1972a. The breeding cycle and growth of open coast and estuarine populations of *Littorina littorea*. *J. mar. biol. Ass. U.K.* 52: 1011–1019. The populations of winkles studied were from Craig-yr-Wylfa near Borth and in the Dyfi estuary.
- , 1972b. The estuarine fauna at Ynyslas. In WATKIN, E. E., *A handbook for Ynyslas*. Nature Conservancy Council and University College of Wales, Aberystwyth. This article describes the physical conditions in the estuary of the River Leri and gives the abundance of *Hydrobia ulvae*, *Retusa obtusa*, *Cerastoderma edule* and *Macoma balthica* along a transect line. *Tellina tenuis* was also present, but in low numbers. An account is also given of the more muddy habitats upstream of the transect where *Hydrobia ulvae*, *Littorina saxatilis* agg., *L. littorea*, *Scrobicularia plana* and *Mya arenaria* were recorded.
- and FISH, S., 1974. The breeding cycle and growth of *Hydrobia ulvae* in the Dovey Estuary. *J. mar. biol. Ass. U.K.* 54: 685–697. Transects were worked at Ynyslas beach and 400 m upstream in a muddier environment. *Hydrobia ulvae* was abundant during the survey (1969–1971) and there was a suggestion that the specimens were larger in the more muddy habitat.
- and ———, 1977a. The veliger larva of *Hydrobia ulvae* with observations on the veliger of *Littorina littorea* (Mollusca: Prosobranchia). *J. Zool. Lond.* 182: 495–503. The egg masses of *Hydrobia ulvae* were obtained from Ynyslas while the veligers of *Littorina littorea* were obtained from plankton samples in Cardigan Bay.
- and ———, 1977b. The effects of temperature and salinity on the embryonic development of *Hydrobia ulvae* (Pennant). *J. mar. biol. Ass. U.K.* 57: 213–218. Egg masses of *H. ulvae* were obtained from Ynyslas beach on the Dyfi estuary.
- FOX, B., 1925 1. *An account of investigations into the fauna of the sub-soil of a flat plain situated between the tidemarks, south of the Dovey estuary.* 2. *The anatomy of the marine triclad Fovis affinis*. M.Sc. Thesis. University College of Wales, Aberystwyth. Results of 83 samples taken at Ynyslas. *Hydrobia ulvae* was by far the most abundant species. *Retusa obtusa*, *Cerastoderma edule*, *Macoma balthica* and *Scrobicularia plana* were also recorded.
- GOODWIN, B. J., 1975. *Studies on the biology of Littorina obtusata and L. mariae* (Mollusca: Gastropoda). Ph.D. Thesis, University College of Wales, Aberystwyth. Specimens were collected from Aberystwyth and New Quay, Dyfed. In addition to Flat Winkles there are records of other species of marine Mollusca found in the same habitat. Some of the thesis is published in GOODWIN and FISH (1977).
- , 1978. The Growth and breeding cycle of *Littorina obtusata* (Gastropoda, Prosobranchiata) from Cardigan Bay. *J. moll. Stud.* 44: 231–242. A population of Flat Winkles was studied at College Rocks, Aberystwyth.
- and FISH, J. D., 1977. Inter- and intraspecific variation in *Littorina obtusata* and *L. mariae* (Gastropoda: Prosobranchia). *J. moll. Stud.* 43: 241–254. Collecting localities included Aberystwyth and New Quay.
- GREENE, C., 1891. Marine Shells of North Wales. *The Conchologist* 1: 1–5. Includes records from the coast of Cardigan Bay north of the Mawddach estuary. Over 100 species are listed.
- , 1906. Conchology in North Wales. In: ROBERTS, A. and WOODALL, E. 1906. *Gossiping guide to Wales (North Wales and Aberystwyth)*. Simpkin, Marshall, Hamilton Kent and Co., London and Woodhall, Minshall Thomas and Co., Oswestry and Wrexham. Lists of species for Mochras (49) and Harlech (13) both of which omit the common species. A footnote mentions a recent summer when many of the species could not be found. An extract from this was produced in the *Conchologists' Newsletter* No. 35, 187–189.
- HAWARD, N. J. B., 1977. *The live and dead shelly fauna and the sediments of outer Cardigan Bay*. Ph.D. Thesis, University College of Wales, Aberystwyth. Dredge samples were taken off-shore from just south of Cardigan to the Llyn peninsula. Live records were noted with some indication of abundance. A total of 37 species of bivalves and 22 species of gastropods was recorded, which included typical sub-littoral species. The thesis also includes information on the bottom substratum which affects the distribution of live molluscs.
- HAYNES, J. and DOBSON, M., 1969. Physiography, foraminifera and sedimentation in the Dyfi estuary (Wales). *Geol. J.* 6: 217–256. Four species of marine molluscs are recorded for the low marsh, 18 species of shells from gravel accumulations at the mouth of the estuary of Ynyslas and 2 species from the main channel. The paper gives a detailed account of the physical features of the environment at the Dyfi estuary.
- HORSMAN, E., 1922. Additions to the marine fauna of Aberystwyth and district. *Aberyst. Stud.* 4: 259–268. Thirteen species of marine molluscs, additional to an earlier list (Walton 1913) are recorded. Details of locality and date of collection are given.
- IRELAND, M. P., 1973. Result of fluvial zinc pollution on the zinc content of littoral and sub-littoral organisms in Cardigan Bay, Wales. *Environ. Pollut.* 4: 27–35. This study includes an analysis of the lead content of molluscs and seawater from seven localities from Constitution Hill, north of Aberystwyth, south to Monk's Cave. Three species of molluscs, *Littorina littorea*, *Nucella lapillus* and *Mytilus edulis* were studied. The levels of zinc varied according to proximity to polluted river waters and the different feeding habits of the molluscs.
- and WOOTTON, R. J., 1977. Distribution of lead, zinc, copper and manganese in the marine gastropods, *Thais lapillus* and *Littorina littorea* around the coast of Wales. *Environ. Pollut.* 12: 27–41. The bodies and shells of molluscs were analysed for heavy metals from samples taken at Criccieth, Barmouth, Aberystwyth and New Quay.
- JAMES, B. L., 1964a. The life cycle of *Parvatrema homoeotecnium* sp. nov. (Trematoda, Digenea) and a review of the family Gymnophallidae Morozov, 1955. *Parasitology* 54: 1–41. Various stages of the life cycle of this larval fluke were



- found in the haemocoel of *Littorina saxatilis* subsp. *tenebrosa*.
- , 1964b. *Studies on larval trematodes from some littoral molluscs*. Ph.D. Thesis, University College of Wales, Aberystwyth. Most of this thesis is published as papers.
- , 1968a. The characters and distribution of the subspecies and varieties of *Littorina saxatilis* (Olivi 1792) in Britain. *Cah. Biol. mar.* **9**: 143–165. *Littorina saxatilis* agg. were collected from Ynyslas and Aberystwyth. The sub-species are illustrated by photographs.
- , 1968b. The occurrence of larval digenea in ten species of intertidal prosobranch molluscs in Cardigan Bay. *J. nat. Hist.* **2**: 329–343. The study area is between Twr Gwylanod and the Dovey estuary and fieldwork was undertaken from 1958–1960. 10 species of marine molluscs were recorded infected with larval digenea (parasitic flukes) belonging to 15 species. No parasites were found in *Patina pellucida*.
- JAMES, M., 1973. *Ultrastructure and histochemical studies on larval Digenea from marine molluscs*. Ph.D. Thesis, University College of Swansea, University of Wales. *Gibbula umbilicalis* and *Littorina littorea* were collected from Twr Gwylanod near Aberystwyth. *L. littorea* were also collected from Monk's Caves and at Aberystwyth.
- JENKINS, J. T., 1905. Discussion of official fishery statistics. *Rep. Lancs. Sea-Fish. Labs.* (1904) **13**: 1–50. Records landings and financial return from shell-fisheries. Includes reference to winkles at Aberaeron, Llanon and Llanrhystud; cockles at Tre-r-ddol and Ynyslas and mussels at Aberaeron, Aberystwyth and Aberdyfi. All three shell-fish are mentioned for Pwllheli.
- JOHN, G. J., 1940. *Ecology of a rocky shore*. M.Sc. Thesis, University College of Wales, Aberystwyth. Results of transect work on the shore at Aberystwyth. *Patina pellucida* was recorded as common on *Laminaria* and ten other species of molluscs were also noted.
- JOHNSTONE, J., 1914. Report on the examination of various mussel beds in Lancashire and Wales during the year 1913. *Rep. Lancs. Sea-Fish. Labs.* **22**: 353–376. A bacteriological analysis of the seawater and mussels was undertaken at Aberdovey and Barmouth. The mussels were shown to be contaminated, especially in the harbours.
- , 1915. The methods of cleansing living mussels from ingested sewage bacteria. *Rep. Lancs. Sea-Fish. Labs.* **23**: 57–108. The appendix to the paper gives the results of bacteriological tests on mussels from Aberdovey, the Dovey estuary and Barmouth.
- JONES, A. M., 1974. *Studies on the physiology and ecology of Cardium edule and Macoma balthica* (Mollusca: Lamellibranchia). Ph.D. Thesis, University College of Wales, Aberystwyth. Results of a littoral transect at Ynyslas in 1968–1970. *Hydrobia ulvae* and *Retusa obtusa* were recorded in addition to *Cerastoderma edule* and *Macoma balthica*.
- JONES, D. H., 1960. *A preliminary survey of the fauna associated with certain seaweeds occurring on a selected area of shore near Aberystwyth*. M.Sc. Thesis, University College of Wales, Aberystwyth. The study area was just to the north of Aberystwyth and a description of the habitat was included in the thesis. The following molluscs were recorded: *Anomia ephippium*, *Mytilus edulis*, *Modiolus* sp., *Lasaea rubra*, *Patina pellucida*, *Littorina littoralis*, *L. saxatilis*, *L. neritoides*, *Lacuna* sp., *Rissoa* sp. and *Utriculus* sp. Bivalves were more common on the seaweeds than gastropods.
- LAURIE, R. D. and WATKIN, E. E., 1922. Investigations into the fauna of the sea floor of Cardigan Bay. A preliminary account of work in the northern portion of a region between Aberystwyth and New Quay known as the 'Gutter'. *Aberyst. Stud.* **4**: 229–249. Records 18 species of marine Mollusca which were off-shore species collected in grab samples. The numbers of specimens collected is recorded and there is additional information on some of the species.
- LEWIS, J. R. and POWELL, H. T., 1961. The occurrence of curved and unguulate forms of the mussel *Mytilus edulis* L. in the British Isles and their relationship to *M. galloprovincialis* Lamarck. *Proc. zool. Soc. Lond.* **137**: 583–598. The paper outlines the differences between *Mytilus edulis* and *M. galloprovincialis* using both shell characters and the animal: it concludes that *M. galloprovincialis* is probably only a sub-species. Mussels with some development of beaking are recorded from Aberystwyth.
- MOORE, C. H., 1909. Shell-collecting in the Barmouth district. *J. Conch., Lond.* **12**: 294–295. Reports on the area being poor for marine shell collecting. Three common shells were recorded for Harlech. Mochras was reported as poor; fifteen species collected there are listed.
- MORGAN, T. O., 1851. *New guide to Aberystwyth and its environs*. J. Cox, Aberystwyth. Includes a Conchology section on page 166 which lists 28 genera from Borth Sands and Aberdovey. Species names are not given.
- MOYSE, J. and NELSON-SMITH, A., 1964. Effects of the severe cold of 1962–63 upon shore animals in South Wales. *J. Anim. Ecol.* **33**: 183–190. Refers to the effects of the cold on *Monodonta lineata* and *Gibbula umbilicalis* at Aberystwyth.
- NATURE CONSERVANCY COUNCIL, 1970. *Ynyslas Nature Reserve: Field Studies*. Nature Conservancy Council, South Wales Region. Nine species of marine and brackish water molluscs are listed for the Dyfi estuary.
- OWEN, M., 1935. *The faunal communities of an inter-tidal plain*. M.Sc. Thesis, University College of Wales, Aberystwyth. The study area was on the south shore of the Dyfi estuary at Ynyslas. *Hydrobia ulvae*, *Littorina littorea*, *Retusa obtusa*, *Mytilus edulis*, *Cerastoderma edule*, *Macoma balthica* and *Scrobicularia plana* are recorded.
- PASCOE, D., 1968. *Studies on the metabolism of Digenea from sea birds and molluscs*. Ph.D. Thesis. University College of Swansea, University of Wales. *Littorina littorea* and *L. saxatilis* agg. were collected from Twr Gwylanod, south of Aberystwyth.
- PYEFINCH, K. A., 1943. The intertidal ecology of Bardsey Island, North Wales, with special reference to the recolonization of rock surfaces and the rock-pool environment. *J. Anim. Ecol.* **12**: 82–108. Records the results of fieldwork undertaken during the summers of 1936, 1937 and 1938 on a rocky coast with brown seaweeds and two small areas of sand. Twenty-three species of marine molluscs were recorded. Some rock surfaces were denuded of



- life and the subsequent recolonization followed. Eight species of molluscs were recorded from the rock-pools.
- RACK, E. H., 1924. (1) *The biology of the sand*. (2) *Additions to the marine fauna of Aberystwyth and district*. Ph.D. Thesis. University of Wales. Part 1 of the Thesis was a study of the Dyfi estuary at Ynyslas where *Hydrobia ulvae* was the dominant mollusc. *Cerastoderma edule* and *Mytilus edulis* were also recorded. See also Horsman, 1922.
- REES, W. J., 1936. Note on the ubiquitous cercaria from *Littorina rudis*, *L. obtusata* and *L. littorea*. *J. mar. biol. Ass. U.K.* **20**: 621–624. The paper mostly concerns the parasites found in the three species of winkles which were collected from Aberystwyth in 1935.
- ROBERTS, T., 1976. *Detailed guide to the beaches of Pembrokeshire, Cardiganshire and Carmarthenshire*. Abercastle Publications, Abercastle, Dyfed. A useful description of some beaches in this region with information on access.
- SCARRATT, D. J., 1961. *The fauna of Laminaria holdfasts*. Ph.D. Thesis, University College of Wales, Aberystwyth. A few samples of *Laminaria* collected from Aberystwyth yielded *Patina pellucida*, *Gibbula cineraria* and *Odostomia spiralis*.
- SMITH, S. M., 1976. Recorder's report: marine Mollusca. *J. Conch., Lond.* **29**: 122–124. *Limapontia depressa* is recorded for Census Area 22.
- STRICKLAND, H. E., 1834. A list of the more rare species of shells, which were collected in August, 1833, at Aberdovey in Merionethshire. *Ann. Mag. nat. Hist.* **7**: 159–160. The list of names includes foraminifera as well as molluscs. There are species with very small shells (e.g. *Cingula* spp. and *Odostomia* spp), so the author must have collected from shell sand. He also records Top Shells from rocks at Aberystwyth.
- TOMLIN, J. R. le B., 1892. Notes on the marine Mollusca of the North Wales coast, with complete lists of the recorded nudibranchs and cephalopods. *J. Conch., Lond.* **7**: 25–31. Tomlin includes some records with specific localities from the coast of Cardigan Bay as far south as the Dyfi estuary.
- TURK, S. M., 1970 (No title) *Conchologists' Newsletter* **34**: 163–164. A list of records of marine molluscs for Cardigan Bay (Marine Census Area 22) with notes on the status of the record and the age of the record (nineteenth or twentieth century).
- WALTON, C. L., 1913a. The shore fauna of Cardigan Bay. *J. mar. biol. Ass. U.K.* **10**: 102–113. The paper gives a description of the shore-line and conditions affecting the fauna. Some 47 species of marine molluscs are listed and of these only 11 were bivalves. The list is annotated with locality data and occasional notes on habitat and abundance. This region has a restricted molluscan fauna.
- , 1913b. The distribution of some littoral Trochidae and Littorinidae in Cardigan Bay. *J. mar. biol. Ass. U.K.* **10**: 114–122. This paper investigates the local distribution of Winkles and Top Shells from Gwbert-on-sea in the south of Cardigan Bay to Pwllheli in the north. The species studied were: *Gibbula cineraria*, *G. umbilicalis*, *G. magus*, *Monodonta lineata*, *Calliostoma zizyphinum*, *Littorina littorea*, *L. neritoides*, *L. littoralis* agg. and *L. saxatilis* agg. Environmental factors which may affect the distribution of these species are discussed.
- , 1913c. The mussel and cockle industries of Cardigan Bay. *Report on Investigations towards the Improvement of Fisheries in Cardigan Bay and its Rivers*. Zoological Department, University College of Wales, Aberystwyth. (This paper is part of a collection of published works submitted for the degree of M.Sc. in 1914 at University College of Wales, Aberystwyth). A report on the present state of shell-fish beds at the Dyfi estuary (mussels and cockles), Barmouth (mussels and a few cockles which were not exploited) and Portmadoc (mussel fishing from boats). Some economic statistics are given. Most of the cockles were eaten locally as long-distance marketing was not economic with the small quantity of shell-fish involved, and the blackened shells of cockles from mud made the produce less marketable than cockles with clean shells.
- , 1920. A contribution to the ecology of some cockle beds. *Rep. Lancs. Sea-Fish. Labs.* **28**: 34–46. This paper includes some lists of the marine molluscan fauna from named study areas including Cardigan Bay. There is a section on the cockle population at Ynyslas.
- WHATLEY, R. C., 1975. *The Mollusca of Ynyslas and the Dyfi Estuary*. Information sheet. Natural Environment Research Council. A very general account aimed at the general public rather than the conchologist. Some of the common species are mentioned by name.
- WILLIAMS, D. C., 1938. *The anatomy, feeding mechanism and growth of Macoma balthica* (L.). M.Sc. Thesis. University College of Wales, Aberystwyth. The animals studied came from the Dyfi estuary at Ynyslas. The thesis includes observations on the growth rate and spat-fall (from monthly samples) during 1936–7.
- WILLIAMS, E. E., 1963. *Studies on selected intertidal gastropods*. Ph.D. Thesis, University College of Wales, Aberystwyth. *Gibbula umbilicalis*, *Monodonta lineata* and *Littorina littorea* were studied at monthly intervals at Borth. Much of this thesis is published. (Williams, 1964a, 1964b).
- , 1964a. The growth and distribution of *Littorina littorea* (L.) on a rocky shore in Wales. *J. Anim. Ecol.* **33**: 413–432. Records the results of a beach transect studied from 1961–1963 at Craig-yr-Wylfa, just south of Borth.
- , 1964b. The growth and distribution of *Gibbula umbilicalis* (da Costa) on a rocky shore in Wales. *J. Anim. Ecol.* **33**: 433–442. Records the results of field work on a population of *Gibbula umbilicalis* studied from 1961–1963 at Tanybwllch to Alltwen, south of Aberystwyth. The presence of *Monodonta lineata*, *Littorina littorea* and *L. saxatilis* agg. was also recorded.

NORTH WALES. (Counties of Gwynedd and Clwyd) Marine census areas 23 and 24.

ALI, R. M., 1971. *Factors influencing rates of filter feeding in marine bivalves*. Ph.D. Thesis. University College of North Wales,



- Bangor. *Cerastoderma edule* was collected from Garth beach, Bangor, whilst some other animals used in the experiments were obtained from the fisheries laboratory at Conwy.
- ANON, 1926. Shells from the shore between Penmaenmawr Headland and Aber. *Proc. Llandudno Distr. Fld. Club.* **11**: 133–138. Thirty six species of bivalves and 22 species of gastropods are recorded with notes on habitat and abundance.
- ARCHER, F., 1892. Supplementary report upon the testaceous Mollusca of the L.M.B.C. district. *Trans. L'pool. Biol. Soc.* **6**: 105–121. An annotated species list with localities and other notes which include reference to marine Mollusca in North Wales.
- BAIRD, R. H., 1966. Factors affecting the growth and condition of mussels (*Mytilus edulis* L.). *Fishery Invest., Lond.* Ser. 2, **25** (2): 1–33. This paper includes a map of the mussel beds in the mouth of the Conwy. It also compares the growth and form of mussels from different tidal levels.
- BERRY, R. J. and CROTHERS, J. H., 1974. Visible variation in the dog-whelk, *Nucella lapillus*. *J. Zool., Lond.* **174**: 123–148. Includes reference to populations of dog-whelks in North Wales.
- BLAKE, W., 1923. Observations on the Molluscan Life of Llanfairfechan shore. *Proc. Llandudno Dist. Fld. Club* **9**: 34–43. An account of the results from shore collecting on ten-day visits to Llanfairfechan in 1921 and 1923. Forty three species of marine molluscs are listed, of which the majority is bivalves.
- BOADEN, P. J. S., 1963. The interstitial fauna of some North Wales beaches. *J. mar. biol. Ass. U.K.* **43**: 79–96. Beaches on the Llyn peninsula and at Llanfairfechan were studied, but there is no record of the localities in which each species was found.
- BULSTRODE, H. T., 1911. *Report on shell-fish other than oysters in relation to disease*. H.M.S.O., London. This paper gives locations of mussel and cockle beds in Wales with a good deal of background information on the shell-fish industry. The Conway mussels are included.
- COLLINGWOOD, C., 1860. On the nudibranchiate Mollusca inhabiting the estuary of the Dee. *Ann. Mag. nat. Hist.* Ser. 3, **6**: 196–202. Lists 24 species on the Cheshire side of the Dee estuary.
- COWELL, E. B. and CROTHERS, J. H., 1970. On the occurrence of multiple rows of 'teeth' in the dog-whelk *Nucella lapillus* (L.) *J. mar. biol. Ass. U.K.* **50**: 1101–1111. Lists a few populations of dog-whelk in North Wales.
- CRISP, D. J., 1964. Mortalities in marine life in North Wales during the winter 1962–63. *J. Anim. Ecol.* **33**: 190–197. Observations made during field courses before the hard winter are compared with those from field work immediately after the severe cold. Distribution maps also showing the abundance of *Monodonta lineata* and *Gibbula umbilicalis* before and after the hard winter are given. There is further information in the text on the effect of the severe winter on other species of molluscs.
- CRISP, L. J., 1952. Marine biology in North Wales. *Proc. Llandudno Dist. Fld. Club.* **25**: 15–22. Gives an account of the history of marine biology in North Wales starting with Thomas Pennant. The work of the Liverpool Marine Biological Committee under Professor Herdman is outlined and the establishment of their marine laboratories first at Puffin Island off Anglesey and later at Port Erin, Isle of Man. The paper concludes with the new marine laboratory at Menai Bridge.
- CROTHERS, J. H., 1971. Further observations on the occurrence of 'teeth' in the dog-whelk *Nucella lapillus*. *J. mar. biol. Ass. U.K.* **51**: 623–639. Includes localities of some populations of *Nucella lapillus* in North Wales studied in 1969–70.
- DARBISHIRE, R. D., 1886. *Report on the testaceous Mollusca of the L.M.B.C. district. The first report upon the fauna of Liverpool Bay and the neighbouring seas*. Liverpool Marine Biological Committee. Includes reference to marine molluscs on the beaches of North Wales and also off-shore.
- DARE, P. J., 1966. The breeding and wintering population of the oystercatcher (*Haematopus ostralegus*) in the British Isles. *Fishery Invest., Lond.* Ser. 2, **25** (5): 1–69. Includes reference to populations of oystercatchers in North Wales with a list of recorded foods. Fifteen different species of molluscs are known to be taken as food in localities in Britain and Europe.
- and EDWARDS, D. B., 1975. Seasonal changes in fresh weight and biochemical composition of mussels (*Mytilus edulis* L.) in the Conwy Estuary, North Wales. *J. exp. mar. Biol. Ecol.* **18**: 89–97. Sublittoral mussels were dredged from natural beds in the Conwy estuary (1971–1974).
- DEAN, J. D., 1935. Type localities of British Mollusca. *J. Conch., Lond.* **20**: 176–179. Refers to Pennant's type locality for *Hydrobia ulvae* in Flintshire and his locality for *Solen marginatus* Montagu (recorded by Pennant as *S. vagina*). The early records of *Monodonta lineata* made by da Costa are listed.
- DEE ESTUARY CONSERVATION GROUP, 1976. *The Dee Estuary. A surviving wilderness*. A general and illustrated account of the Dee estuary, but including some information on the marine molluscs and their use as food by wading birds.
- DESAI, B. N., 1966. The biology of *Monodonta lineata* (da Costa). *Proc. malac. Soc. Lond.* **37**: 1–17. Refers to populations of *Monodonta lineata* at Clynnog and Pont Llyfni.
- DOBSON, M., EVANS, F. and JAMES, K., 1971. The sediments on the floor of the southern Irish Sea. *Marine Geology* **11**: 27–69. This includes data on marine molluscs dredged from stations off the north of the Llyn peninsula. The list of species is given in the appendix.
- DRINNAN, R. E., 1958. The winter feeding of the oystercatcher (*Haematopus ostralegus*) on the edible mussel (*Mytilus edulis*) in the Conwy estuary, North Wales. *Fishery Invest., Lond.* Ser. 2, **22** (4): 1–15. Reports on observations on the feeding behaviour of oystercatchers and the method of attack made during 1955–6 in the estuary of the River Conwy. Each bird was estimated to eat its own weight of shell-fish each day.



- and COLE, H. A., 1957. Oyster catchers (*Haematopus ostralegus*) as pests of cockle and mussel beds. *Nature Wales* **3**: 499–503. Although mostly about the Burry Inlet, this paper refers to oystercatchers feeding on mussels at Conwy.
- ELDERFIELD, M., THORNTON, L. and WEBB, J. S., 1971. Heavy metals and oyster culture in Wales. *Mar. Poll. Bull.* **2** (3): 44–47. Refers to problems in rearing larvae at an oyster hatchery at Conwy and refers to the possible effects of heavy metals in the sea-water.
- FISHER, N., 1936a. The distribution of *Monodonta lineata* (da Costa) in Wales. *N. West. Nat.* **11**: 272. Additional records are given to supplement da Costa's record for *Monodonta lineata* at Pwllheli. Three dead shells 9 miles south west of Caernarvon (1936); the other more recent records were for Anglesey.
- , 1936b. *Monodonta lineata* (da Costa) in North Wales. *J. Conch., Lond.* **20**: 224.
- FLETCHER, A. and JONES, W. E., 1975. *The second report of the Coastal Surveillance Unit*. Bangor: University College of North Wales 109 pp. Further progress since the first report with some transect data including molluscs and particularly winkles and limpets.
- and —, 1976. *The second report of the Coastal Surveillance Unit*. Bangor: University College of North Wales 158 pp. Stations outlined in earlier reports were studied and there is an updated species list for North Wales and Anglesey. Observations are given on results of particular species for the transect and the limpets have continued to receive more detailed study.
- GARNER, R., 1856. On the pearls of the Conway River, North Wales, with some observations on the natural productions of the neighbouring coast. *Rep. Brit. Ass.* (1856) Part 2: 92–93. Refers to pearls in marine mussels. There is some further information on marine molluscs in the Llandudno area and at the mouth of the Conwy.
- GILLESPIE, A. S. 1932. Notes on the sandy shore fauna of Colwyn Bay. *NWest. Nat.* **7**: 23–26. Records the habitat and fauna from Rhos Pier to Victoria Pier, Colwyn Bay. Three marine molluscs are named at the species level and 9 at the genus level.
- GREENE, C., 1891. Marine shells of North Wales. *The Conchologist* **1**: 1–5. A list of marine molluscs resulting from field work in 1881, 1882 and 1889 with additional records incorporated. Localities are given from each species. Fifty nine species are listed for this area of coast.
- , 1906. Conchology in North Wales. In: ROBERTS, A. and WOODALL, E. *Gossiping Guide to Wales (North Wales and Aberystwyth)*. Simpkin, Marshall, Hamilton, Kent and Co. London and Woodhall, Minshall, Thomas and Co. Oswestry and Wrexham. Refers to marine molluscs at Colwyn Bay (37 species) and Penmaenmawr (13 species). Reprinted in 1970 in the *Conchologists' Newsletter* **35**: 187 and 189.
- HARFIELD, L. D., 1969. Census Area 24, a preliminary report. *Conchologists' Newsletter* **29**, 94–97. A list of the marine molluscs from the Liverpool Bay sea area with details on the status of each record. This list is included here since it includes the Dee estuary and part of the North Wales coast and as it is the adjacent marine census area.
- HELLER, J., 1975. The taxonomy of some British *Littorina* species, with notes on their reproduction. (Mollusca: Prosobranchia). *Zool. J. Linn. Soc.* **56**: 131–151. This paper divides *Littorina saxatilis* agg. into four species. Some of the collections of winkles on which the work is based were collected from the Llyn peninsula.
- HERDMAN, W. A., 1886. *Report on the Nudibranchiata of the L.M.B.C. district. The first report upon the fauna of Liverpool Bay*. Liverpool Marine Biological Committee. Longmans Green and Co. pp. 267–277. An annotated list of 14 species of sea slugs from the coast of North Wales.
- , 1894. Notes on the submarine deposits of the Irish Sea. *Proc. L.pool geol. Soc.* **7**: 171–182. An account of bottom deposits including some off the shore of North Wales to a depth of over 50 fathoms. Some marine molluscs are mentioned, including living populations of *Pecten maximus* and *Chlamys opercularis*.
- and CLUBB, J. A., 1889. *Second report on the Nudibranchiata of the L.M.B.C. district. The second report upon the fauna of Liverpool Bay and the neighbouring seas*. Liverpool Marine Biological Committee. Records one new species for Penmaenmawr.
- and —, 1892. *Third report upon the Nudibranchiata of the L.M.B.C. district. The third volume of reports upon the fauna of Liverpool Bay and the neighbouring seas*. Liverpool Marine Biological Committee. pp. 131–169. This report includes new localities for seaslugs and records 16 species from the coast of North Wales.
- HOLDEN, M. J., WOOD, R. J. and EDWARDS, E., 1975. Commercial fish, shellfish and pelagic fish of Liverpool Bay. In: *Liverpool Bay. An assessment of present knowledge compiled by members of the Liverpool Bay Study Group*. The Natural Environment Research Council. Series C, **14**: 58–63. Gives an account of the mussel and scallop fisheries. The Edible Mussel *Mytilus edulis* is collected from natural populations in the Conwy Estuary and the Ogwen River. Wales is rated as one of the most important mussel producing centres in the British Isles. North Wales is not listed as a base for commercial Scallop fishing.
- HUGHES, R. N., 1968. *The population ecology and energetics of Scrobicularia plana* (da Costa). Ph.D. Thesis. University College of North Wales, Bangor. Studies on feeding, reproduction, population dynamics and energy budget of *Scrobicularia plana* at Aber foreshore, Conwy Bay. Much of this Thesis is now published.
- , 1970. Population dynamics of the bivalve *Scrobicularia plana* (da Costa) on an inter-tidal mud-flat in North Wales. *J. Anim. Ecol.* **39**: 333–356. *Scrobicularia plana* and *Macoma balthica* are recorded from Aber in the Conwy Bay (SH/645731).
- , 1971. Reproduction of *Scrobicularia plana* Da Costa (Pelecypoda: Semelidae) in North Wales. *Veliger* **14**: 77–81. Regular collections of specimens were made from the Aber foreshore, Conwy Bay. The seasonal development of the



gonads and spawning was investigated by means of histological work in the laboratory.

- IRELAND, M. P. and WOOTTON, R. J., 1977. Distribution of lead, zinc, copper and manganese in the marine gastropods, *Thais lapillus* and *Littorina littorea*, around the coast of Wales. *Environ. Pollut.* **12**: 27–41. In North Wales, samples of molluscs for analysis were collected from Llandudno and Llanllyfni south of Caernarvon. The heavy metal content of the molluscs in the Llanllyfni area is thought to be due to natural pollution from mineral-enriched freshwater run-off, but in general terms these localities in North Wales had a lower total metal concentration in the molluscs compared with samples from other parts of Wales. The level of metals in the tissues and shell from any one site were different in the two species.
- JAMES, K. H., 1973. *Recent sediments and shelly fauna of the Caernarvon Bay region, Southern Irish Sea*. Ph.D. Thesis. University College of Wales, Aberystwyth. The study area includes stations off the Lleyen peninsula and a number of marine molluscs is recorded. See also Dobson, Evans and James, 1971.
- JOHNSTONE, J., 1915. The methods of cleansing living mussels from ingested sewage bacteria. *Rep. Lancs. Sea-Fish. Labs.* **23**: 57–108. The appendix gives the results of bacteriological tests on mussels from Conway.
- JONES, W. E., FLETCHER, A., HISCOCK, K. and HAINSWORTH, S., 1975. *The first report of the Coastal Surveillance Unit*. Bangor: University College of North Wales 39 pp. This report outlines the programme of work and the position of survey sites, which include the Lleyen Peninsula (Porth Dinllaen) and three along the southern shore of the Menai Straits (Penmaenmawr, Penrhyn Castle and Porth Swtan). There is an animal check list, but this includes both Anglesey and North Wales.
- JONES, W. E., FLETCHER, A., BENNELL, S. J., MCCONNELL, B. J., MACKSMITH, S., MITCHELL, J., ROBERTS, C. M., 1977. *The fourth report of the Coastal Surveillance Unit*. Bangor: University College of North Wales 232 pp. The results of the fauna studies for the last three years are discussed together with an updated check list.
- LEWIS, A. H., 1969. *The cold tolerance of inter-tidal animals*. M.Sc. Thesis. University College of North Wales, Bangor. *Littorina neritoides* is recorded for Black Rock Sands.
- LINGWOOD, P., 1976a. The marine Mollusca of Liverpool Bay (Irish Sea). *J. Conch., Lond.* **29**: 51–56. The area of study covered by this paper includes the Dee estuary and the coast of North Wales westwards to Great Orme's Head near Llandudno. A check-list of marine Mollusca is given. This paper also compares the distribution of dead shell assemblages and living mollusc populations with reference to the transportation of dead shells.
- , 1976b. *Intertidal flora and fauna of Llandudno Bay*. Information Sheet, Merseyside County Museums. 2 pp. A very general introduction to the marine life with illustrations of 11 common species of molluscs.
- , 1976c. *The biostratigraphy of some Recent molluscan communities in Liverpool Bay*. Ph.D. Thesis. University of Liverpool. This thesis sets out to discover the relationship between the living marine molluscan populations and assemblages of empty shells. The study area includes the north east coast of Wales from the Dee estuary to Great Orme's Head. Maps showing the distribution of living populations are given for *Macra corallina*, *Venus striatula*, *Donax vittatus*, *Tellina fabula*, *Macoma balthica*, *Cerastoderma edule*, *Pharus legumen*, *Abra alba*, *Barnea candida* and *Mytilus edulis*. These are related to the type of shore and bottom material off-shore. Data on the mollusc populations are analysed by computer. The second part of the thesis is concerned with methods of shell transport. A systematic list to the species in the study area is given in the Appendix.
- LOWE, W. B., 1927. Conchology (shells). *Proc. Llandudno Dist. Fld. Club* **13**: 95. Records *Tellina fabula*, *Cultellus pellucidus* and *Ensis siliqua* for Llanfairfechan.
- McMILLAN, N. F., 1937. Marine Mollusca at Belan Fort, Foryd Bay, Caernarvonshire. *NWest. Nat.* **12**: 401–402. *Gibbula umbilicalis*, *Monodonta lineata*, *Littorina littorea*, *L. saxatilis*, *L. littoralis*, *Hydrobia ulvae*, *Nucella lapillus*, *Facelina drummondi*, *Ovatella myosotis*, *Mytilus edulis*, *Cerastoderma edule* and *Scrobicularia plana* are recorded together with notes on habitat and abundance.
- , 1944. The distribution of *Monodonta* (*Trochus*) *lineata* (da Costa) in Britain. *NWest. Nat.* **19**: 290–292. Includes a list of localities for this species in North Wales.
- , 1946. *Limapontia depressa* Alder and Hancock in North Wales. *J. Conch., Lond.* **22**: 220. *Limapontia depressa* is recorded from a salt-marsh on the Welsh shore of the Dee estuary.
- , 1947. *Phytia myosotis* (Drap.) in Flintshire. *J. Conch., Lond.* **22**: 264. Records *Ovatella myosotis* from a salt-marsh at Point of Air, together with *Hydrobia ulvae*.
- NATURAL ENVIRONMENT RESEARCH COUNCIL, 1975. *Liverpool Bay. An assessment of present knowledge compiled by members of the Liverpool Bay Study Group*. N.E.R.C. Series C, **14**: 72 pp. This includes the north coast of Wales from the Dee estuary west to the Conwy estuary. There is a general report on the benthic and littoral fauna.
- OLDHAM, C., 1930. The shell-smashing habit of gulls. *Ibis*. ser. 12, **6**: 239–243. Records herring gulls dropping mussels at Llanddulas in North Wales.
- PERKINS, E. J., 1956. The fauna of a sand-bank in the mouth of the Dee estuary. *Ann. Mag. nat. Hist.* Ser. 12, **9**: 112–128. Results of a series of transects. *Tellina tenuis*, *Macoma balthica*, *Cerastoderma edule*, *Littorina littorea* and *Hydrobia ulvae* are recorded.
- RAFFAELLI, D. G., 1978. The relationship between shell injuries, shell thickness and habitat characteristics of the intertidal snail *Littorina rudis* Maton. *J. moll. Stud.* **44**: 166–170. *Littorina rudis* Maton was collected from three sites on the Lleyen peninsula and from Aber and Llanfairfechan on the north coast.
- REES, E. I. S., 1973. Inshore Benthos and Sediment Investigation. In: *Out of sight out of mind* **3**, Appendix C: 81–95. Department of the Environment, H.M.S.O. An account of additional grab samples taken in 1971–2 to investigate



the effect of movement of particulate matter on to the coast of North Wales. *Abra alba* was recorded as thriving in organically enriched situations. Associations of species included in dendrogram diagrams included *Mysella bidentata*, *Tellina fabula* and *Abra alba*.

- , 1975. Benthic and littoral fauna of Liverpool Bay. In: *Liverpool Bay. An Assessment of present knowledge*. The Natural Environment Research Council. Series C, **14**: 50–54. A summary of the marine habitats found in the area with a general indication of the distribution of 14 common species of marine molluscs. Much of the early information for this area was assembled by the Liverpool Biological Society in the late 19th century and early 20th century.
- , WALKER, A. J. M. and WARD, A. R., 1972. Benthic Fauna in relation to Sludge Disposal. In: *Out of sight out of mind* **2**, Appendix 14: 297–343. Department of the Environment, H.M.S.O. The results of a survey undertaken in Liverpool Bay in 1970 to assess the effect of sludge deposited in the sea. The account refers to Liverpool Bay in general and only a few of the sampling stations were along the Welsh coast, off Colwyn Bay. No specific data is given on the molluscs apart from a contour map of bivalve density.
- SAVAGE, R. E., 1956. The great spatfall of mussels (*Mytilus edulis* L.) in the River Conway estuary in spring 1940. *Fishery Invest., Lond.* Ser. 2, **20** (7): 1–22. The young mussels settled in great density and smothered the older ones which resulted in a poor harvest and a close-down of the mussel fishery. The growth of the mussels was followed from 1940 to 1945.
- SAVIDGE, J. P., 1964. Severe winter of 1962–3. *Proc. Lpool. Nat. Fld. Club.* (1961–1963): 8–15. A report on the effect of the severe winter on the marine fauna of the coasts of Lancashire and North Wales. Extensive banks of dead shells were washed up on the beaches. *Ostrea edulis*, *Cerastoderma edule*, *Ensis* sp., *Pharus legumen*, *Gibbula umbilicalis* and *Monodonta lineata* were severely affected whilst lower mortalities were reported for *Mytilus edulis*, *Anomia ephippium*, *Spisula solida*, *Scrobicularia plana*, *Lutraria lutraria* and *Patella vulgata*.
- STOPFORD, S. C. D., 1949. *A biological survey of the Dee estuary*. M.Sc. Thesis. The University of Leeds. The survey is limited to the north bank (the English side) from Burton Marshes to Hilbre Point. *Littorina littorea*, *L. saxatilis*, *Hydrobia ulvae*, *Mytilus edulis*, *Cerastoderma edule*, *Macoma balthica*, *Tellina tenuis*, *Scrobicularia plana*, *Abra alba* and *Mya arenaria* are recorded.
- THOMAS, H., 1909. Ramble on the shore beneath the Great Orme. *Proc. Llandudno Distr. Fld. Club* **2**: 39. A brief report of a field meeting. Records the presence of *Doris tuberculata* and great variability in *Nucella lapillus*.
- THOMPSON, I. C., 1886. *First report on the marine fauna in the neighbourhood of Penmaenmawr. The first report upon the fauna of Liverpool Bay and the neighbouring seas*. Liverpool Marine Biological Committee: 315–317. Records *Philine aperta* and *Trivia* sp. at Penmaenmawr.
- TOMLIN, J. R. le B., 1892. Notes on the marine Mollusca of the North Wales coast, with complete lists of the recorded nudibranchs and cephalopods. *J. Conch., Lond.* **7**: 25–31. Essentially this list adds to that of Greene, published in 1891. Tomlin gives a list of 67 species from North Wales (as far south as Barmouth) and Anglesey. Some specific localities and details of abundance are given.
- WALNE, P. R., 1972. The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves. *J. mar. biol. Ass. U.K.* **52**: 345–374. The results of experimental work on 5 species of bivalves maintained in experimental cultures at Conwy. The *Mytilus edulis* was native to Conwy, but the other species were brought in from elsewhere.
- WILSON, D. P., 1977. *Modiolus modiolus* (L.) in small tidal rock pools at Penrhyn, North Wales. *Est. coast. mar. Sci.* **5**: 215–222. This paper describes a population of *Modiolus modiolus* living in pools in limestone boulders on the shore at Rhos-on-Sea (23/841812) which have been studied by the author over a period of 50 years. Large populations of a few common species of littoral molluscs were also recorded: these included *Patella vulgata*, *Littorina littorea*, *Nucella lapillus* and *Mytilus edulis*.
- , 1977. The stability during many years of the mid tidal shore at Penrhyn Bay, North Wales, and a note on the peat beds at Rhos-on-Sea. *Est. coast. mar. Sci.* **5**: 209–213. This paper is mostly on the physical nature of the shore but two bivalves *Barnea candida* and *Zirfaea crispata* were recorded alive in the peat bed in 1945.

#### ANGLESEY AND THE MENAI STRAITS. (County of Gwynedd) Marine Census Area 23).

- ALI, R. M., 1970. The influence of suspension density and temperature on the filtration rate of *Hiatella arctica*. *Marine Biology* **6**: 291–304. *Hiatella arctica* was collected from calcareous rock near low water at Penmon beach, Anglesey.
- , 1971. *Factors influencing rates of filter feeding in marine bivalves*. Ph.D. Thesis. University College of North Wales, Bangor. *Modiolus modiolus*, *Laevicardium crassum* and *Tellina crassa* were collected at Puffin Island; *Mytilus edulis* off Cadnant, Menai Straits and Menai Bridge; *Crassostrea gigas* from the oysterage at Tal-y-Foel; *Arctica islandica* from the west coast of Anglesey and *Venus striatula* from Red Wharf Bay.
- ANON., 1932. Practical marine biology. *NWest. Nat.* **7**: 277–8. An account of a field course. *Aplysia* was recorded from *Zostera* beds at Tre-Arddur Bay, Anglesey.
- ARCHER, F., 1892. *Supplementary report upon the testaceous Mollusca of the L.M.B.C. district. The third report upon the fauna of Liverpool Bay and the neighbouring seas*. Liverpool Marine Biological Committee. 59–75. Includes records from Puffin Island and Anglesey.
- BAYNE, B. L., 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *J. Anim. Ecol.* **33**: 513–523. A study of spatfall at Tal-y-Foel on the Menai Straits with mussels attaching first to seaweeds and later to mussel beds.



- BAIRD, R. H., 1966. Notes on the scallop (*Pecten maximus* L.) population in Holyhead Harbour. *J. mar. biol. Ass. U.K.* **46**: 33–47. A map is given showing the distribution of scallops in Holyhead harbour together with some data on the age composition of the population and recruitment by spat settlement.
- BERRY, R. J. and CROTHERS, J. H., 1974. Visible variation in the dog whelk, *Nucella lapillus*. *J. Zool., Lond.* **174**: 123–148. The list of localities includes Anglesey and the Menai Straits.
- BOADEN, P. J. S., 1961. Littoral Interstitial Species from Anglesey representing Three Families new to Britain. *Nature, Lond.* **191**: 512. Records a nudibranch *Pseudovermis* from Traeth Bychan, Anglesey.
- , 1962. *Some aspects of the interstitial fauna of sandy beaches*. Ph.D. Thesis. University College of North Wales, Bangor. Much of this Thesis is now published. See Boaden, 1963.
- , 1963. The interstitial fauna of some North Wales beaches. *J. mar. biol. Ass. U.K.* **43**: 79–96. This paper gives the results of a study of the interstitial fauna (very small animals living amongst sand grains) from 21 beaches on Anglesey. The following little-known species of marine molluscs were recorded: *Embletonia faurei* Labbé, *Hedylopsis* sp., *Philinoglossa remanei* Marcus and Marcus and *Pseudovermis* sp.
- CAREFOOT, T. H., 1966. *Growth and nutrition of opisthobranch molluscs*. Ph.D. Thesis. University College of North Wales, Bangor. *Dendronotus frondosus* and *Archidoris pseudoargus* were collected from the Menai Straits, whilst *Aplysia punctata* was collected from Trearddur Bay, Anglesey. Much of this Thesis is now published.
- , 1967a. Studies on a sublittoral population of *Aplysia punctata*. *J. mar. biol. Ass. U.K.* **47**: 335–350. Frequency histograms are given for monthly collections of *Aplysia punctata* from Trearddur Bay (1964–1965). A map is given showing the location of the sublittoral population.
- , 1967b. Growth and nutrition of three species of opisthobranch molluscs. *Comp. Biochem. Physiol.* **21**: 627–652. *Dendronotus frondosus* and *Archidoris pseudoargus* were collected from rocky inter-tidal areas in the Menai Straits. *Aplysia punctata* was collected from a sublittoral population in Trearddur Bay.
- , 1967c. Growth and nutrition of *Aplysia punctata* feeding on a variety of marine algae. *J. mar. biol. Ass. U.K.* **47**: 565–589. *Aplysia punctata* was collected from Trearddur Bay. The growth rates were compared on different species of algae and the food value of the algae was also investigated.
- COOPER, M. E., 1976. *A sublittoral transect across the Menai Strait with particular reference to currents and the fauna associated with the sponge Halichondria panicea (Pallas)*. M.Sc. Thesis. University College of North Wales, Bangor. Results are given from collecting along a transect line to the east of Telford's suspension bridge, Menai Bridge. The data were compared with those from a similar study by Knight-Jones made 20 years previously. Twenty-two species of molluscs were recorded.
- CREAK, J. E., 1974. *An ecological survey of the sublittoral area adjacent to a power station outfall*. M.Sc. Thesis. University College of North Wales, Bangor. This is a study of the shore at Wylfa Head on the north coast of Anglesey, where stations were investigated on either side of the power station. The thesis includes both physical and biological aspects of the environment with a special investigation into the fauna of holdfasts of the oarweed *Laminaria hyperborea*. Seven species of molluscs are recorded and densities of *Patina pellucida* were studied in greater detail in relation to the outfall current from the power station.
- CRISP, D. J., 1964. Mortalities in marine life in North Wales during the winter of 1962–63. *J. Anim. Ecol.* **33**: 190–197. Records the presence of sea-ice on the east of Anglesey. The effects of the cold winter on a number of species are given together with maps showing the distribution and abundance of *Monodonta lineata* and *Gibbula umbilicalis*.
- and KNIGHT-JONES, E. W., 1954. Discontinuities in the distribution of shore animals in North Wales. *Bardsey Observatory Report* (1954): 29–34. A comparison of the marine fauna from the east and west shores of Anglesey with a discussion of factors influencing the distribution.
- CROTHERS, J. H., 1971. Further observations on the occurrence of 'teeth' in the dog-whelk *Nucella lapillus*. *J. mar. biol. Ass. U.K.* **51**: 623–639. The list of localities of populations of dog-whelks studied (1969–1970) includes Anglesey.
- DARBISHIRE, R. D., 1886. *Report on the testaceous Mollusca of the L.M.B.C. district. The first report upon the fauna of Liverpool Bay and the neighbouring seas*. Liverpool Marine Biological Committee 232–266. Includes records from Puffin Island and the Menai Straits.
- DEAN, J. D., 1935. Type localities of British Mollusca. *J. Conch., Lond.* **20**: 176–179. Includes reference to Pennant's localities for *Cultellus pellucidus* (Pennant) (Red Wharf Bay, Anglesey) and da Costa's records of *Monodonta lineata* (da Costa) on Anglesey and other parts of North Wales.
- DEMETROPOULOS, A., 1964. *Measurement of wave action in relation to the ecology of a rocky shore*. M.Sc. Thesis. University College of North Wales, Bangor. Nine stations were studied at Porth Treacastell, where nine species of molluscs were recorded.
- DESAI, B. N., 1966. The biology of *Monodonta lineata* (da Costa). *Proc. malac. Soc. Lond.* **37**: 1–17. Refers to *Monodonta lineata* at Porth Cwyfan, Anglesey.
- DOBSON, M., EVANS, F. and JAMES, K., 1971. The sediments on the floor of the southern Irish Sea. *Marine Geology* **11**: 27–69. This includes data on marine molluscs dredged from stations off the west of Anglesey. The list of species is given in the appendix.
- EVANS, R. G., 1949. The intertidal ecology of rocky shores in South Pembrokeshire. *J. Ecol.* **37**: 120–139. The marine fauna of Menai Bridge is compared with that of Cardigan Bay and South Pembrokeshire.
- FISHER, N., 1936. The distribution of *Monodonta lineata* (da Costa) in Wales. *NWest. Nat.* **11**: 272. Records *Monodonta lineata* from Rhosneigr (1908) and Holyhead (1936), Anglesey.



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- GIBSON, J. S., 1970. The function of the operculum of *Thais lapillus* (L.) in resisting desiccation and predation. *J. Anim. Ecol.* **39**: 159–168. *Nucella lapillus* was collected from a rocky shore on the Menai Straits.
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*Reprints.* No reprints are available from the author, but copies of this paper are being reprinted with the addition of illustrations and these will be available from The Bookshop, National Museum of Wales, Cardiff CF1 3NP.



# THE MOLLUSCAN FAUNA OF AN EARLY POSTGLACIAL TUFA AT TOTLAND, ISLE OF WIGHT

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(Read before the Society, 21 October 1978)

**Abstract:** Close serial sampling and quantitative analyses of the non-marine molluscan fauna of a tufa at Totland Bay, Isle of Wight, has doubled the number of species known. Several locally extinct forms, notably *Spermodea lamellata*, *Leiostryla anglica* and *Pisidium tenuilineatum*, were present. There was little stratigraphical change in faunal composition, although *Vertigo genesii*, *V. geyeri* and *Succinea oblonga* were detected only in the basal samples. The land fauna is one of closed forest. By comparison with other sites described from southern Britain it is suggested that it belongs to the Flandrian climatic optimum (c.7500-c. 5000 BP)

The tufa (spring chalk) deposit in Totland Bay has been known for well over a century and has attracted much attention (Trimmer, 1854; Forbes, 1856; Bristow, 1862; Reid and Strahan, 1889). Kennard and Warren (1904) re-examined the deposit and increased the list of molluscs recorded from it. No further work was done for over fifty years until A. G. Davis (1955) recorded *Spermodea lamellata*, at that time the most southerly British fossil record for this species.

## EXTENT AND STRATIGRAPHY

The deposit occurs at the top of the cliff, some 20m above sea level, between Headon Hill and Widdick Chine. Early accounts suggest that the tufa was much more extensive in the mid 1850's when it could be traced for 350 m in a north-easterly direction from the base of Headon Hill. By 1890 the section had become overgrown and this is still the case today. Although local patches of rather hard tufa bearing the impressions of thallose liverworts were discovered (1978) on broken ground further round the coast at SZ315865, the principal deposit of soft tufa is of very limited extent; only a small remnant could be located at SZ32128671. It seems likely that further cliff erosion will entirely remove this remaining portion.

The following stratigraphy was seen:-

|                     |                                                                         |
|---------------------|-------------------------------------------------------------------------|
| 0- 20 cm            | Modern soil (overgrown).                                                |
| 20- 70 cm           | Yellowish-brown (Munsell colour 10YR 5/8) silt.                         |
| 70- 80 cm           | Dark brown (10YR 4/4) clay.                                             |
| 80-110 cm           | Partially decalcified tufa (2.5Y 7/4).                                  |
| 110-145 cm          | Calcareous tufa, nodular towards base (5Y 7/2).                         |
| 145 cm <sup>+</sup> | <i>Potamomya</i> sands (Headon Beds; Eocene) Light olive grey (5Y 6/2). |

Fig. 1 shows the uneven nodular base of the tufa and the position of the sampling column. The general sequence recorded roughly corresponds to the measured sections of earlier workers.



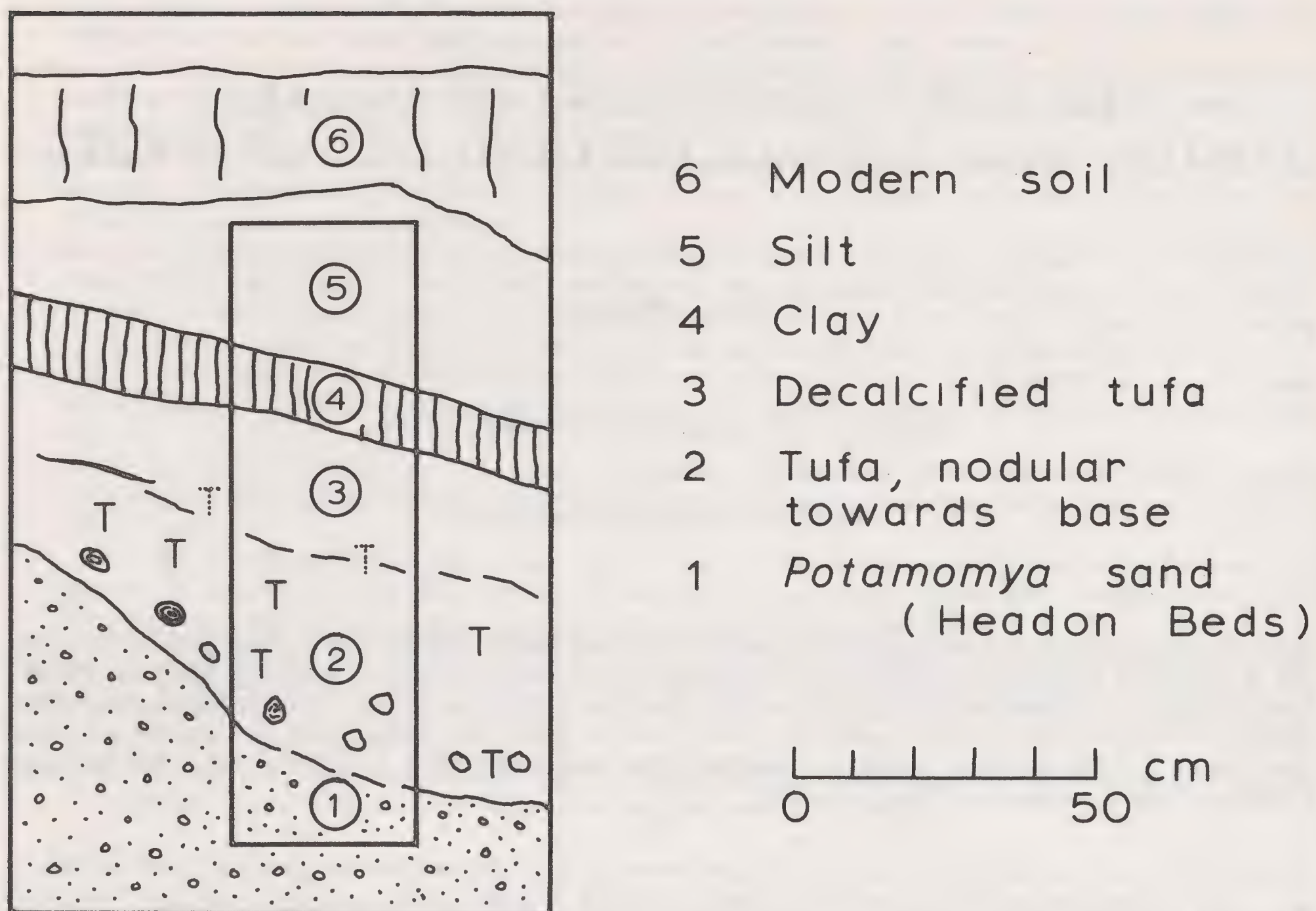


Fig. 1. Profile through Totland tufa (sampling column outlined).

The overlying silt is probably a hillwash and is not the result of decalcification caused by post-depositional weathering.

A series of 5 cm samples were taken from the thickest part of the deposit (Fig. 1). They were dried and 0.5 kg fractions were wet sieved and all fossils above B.S. mesh No. 30 (0.5 mm) extracted. The results are given in Table 1 and plotted graphically in Fig. 2.

To enable direct comparison with similar published snail diagrams certain species have been grouped together into three ecological categories. These are:-

**SWAMP SPECIES** (obligatory hygrophiles) *Carychium minimum*, cf. *Oxyloma pfeifferi*, *Zonitoides nitidus*, *Vertigo antivertigo*, *V. moulinsiana*.

**TERRESTRIAL 'A'** A heterogeneous mixture of essentially catholic species of wide ecological tolerance, occurring in open ground, marshes and coniferous and deciduous woods: *Cochlicopa*, *Columella*, *Punctum*, *Vitrina*, *Vitrea*, *Nesovitrea*, *Limacidae*, *Euconulus*, *Cepaea*, *Arianta*.

**TERRESTRIAL 'B'** Species more critical in their requirements than group 'A' and which are most frequent in deciduous woods and similar well-shaped places: *Carychium tridentatum* (stippled in Fig. 2), *Aegopinella*, *Acanthinula*, *Ena*, *Clausiliidae*. *Carychium tridentatum* and *Aegopinella* form numerically by far the largest part of this group.

Fig. 2. (opposite) Mollusc diagram. Percentages of freshwater and swamp species (open histograms) calculated as independent percentages of total land mollusca.



PREECE: MOLLUSCA OF POSTGLACIAL TUFA AT TOTLAND

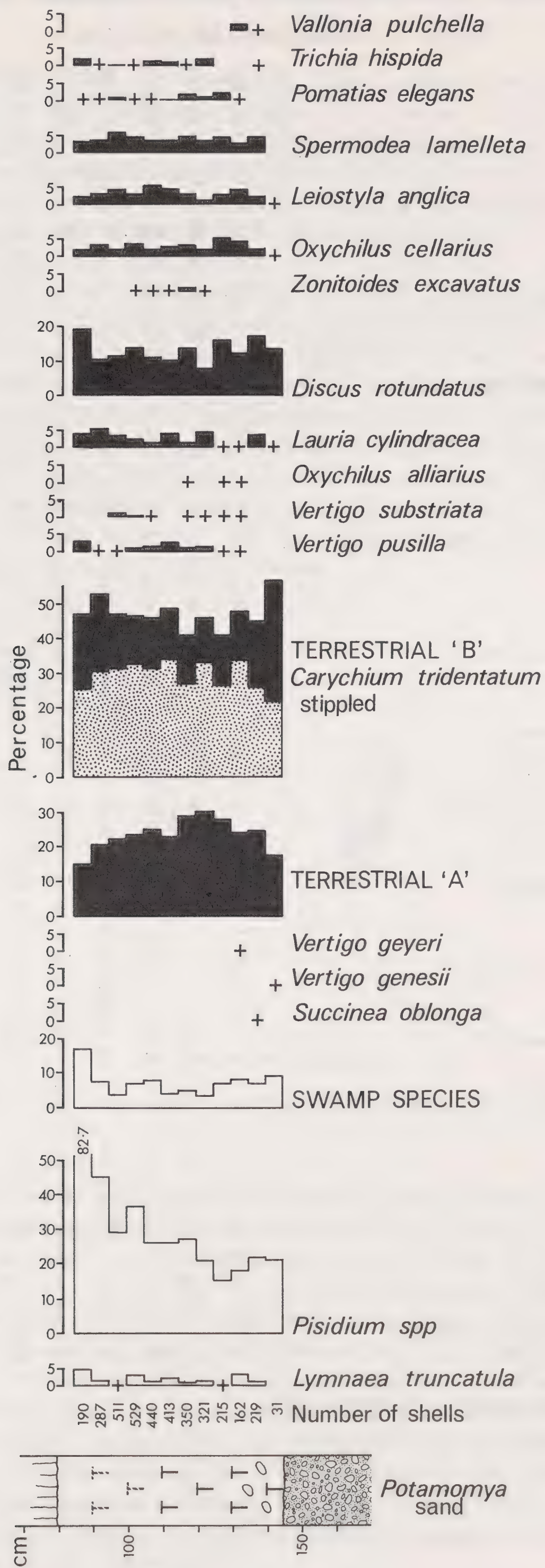




TABLE 1. OCCURRENCE OF MOLLUSCA

| Depth (cm) below surface.                  | 140-150 | 135-140 | 130-135 | 125-130 | 120-125 | 115-120 | 110-115 | 105-110 | 100-105 | 95-100 | 90-95 | 85-90 |
|--------------------------------------------|---------|---------|---------|---------|---------|---------|---------|---------|---------|--------|-------|-------|
| <i>Pomatias elegans</i> (Müller)           | —       | —       | 1       | 3       | 3       | 4       | 2       | 1       | 1       | 3      | 1     | 1     |
| <i>Carychium minimum</i> Müller            | —       | 3       | 3       | 6       | 4       | 5       | 10      | 7       | 9       | 8      | 7     | 4     |
| <i>Carychium tridentatum</i> (Risso)       | 5       | 44      | 42      | 47      | 85      | 70      | 107     | 94      | 117     | 120    | 57    | 24    |
| <i>Lymnaea truncatula</i> (Müller)         | —       | 2       | 4       | 1       | 3       | 2       | 6       | 4       | 12      | 1      | 3     | 4     |
| <i>Succinea oblonga</i> Draparnaud         | —       | 1       | —       | —       | —       | —       | —       | —       | —       | —      | —     | —     |
| cf <i>Oxyloma pfeifferi</i> (Rossmässler)  | 1       | 5       | 4       | 1       | 1       | 3       | 1       | 7       | 10      | 3      | 3     | 11    |
| <i>Cochlicopa lubrica</i> (Müller)         | 1       | 15      | 5       | 11      | 11      | 11      | 15      | 10      | 8       | 16     | 9     | 4     |
| <i>Cochlicopa lubricella</i> (Porro)       | —       | —       | —       | —       | —       | 1       | 1       | —       | —       | 2      | —     | —     |
| <i>Columella edentula</i> (Draparnaud) agg | —       | 2       | 4       | 8       | 12      | 12      | 10      | 13      | 12      | 17     | 2     | 2     |
| <i>Columella aspera</i> Waldén             | —       | +       | +       | +       | +       | +       | +       | +       | +       | +      | —     | +     |
| <i>Vertigo pusilla</i> Müller              | —       | —       | 1       | 1       | 4       | 4       | 7       | 5       | 4       | 1      | 1     | 3     |
| <i>Vertigo antivertigo</i> (Draparnaud)    | —       | —       | —       | 2       | 1       | 2       | —       | 1       | 1       | —      | 2     | —     |
| <i>Vertigo substriata</i> (Jeffreys)       | —       | —       | 1       | 1       | 1       | 1       | —       | 1       | 2       | 4      | —     | —     |
| <i>Vertigo moulinsiana</i> (Dupuy)         | —       | 4       | —       | 1       | 1       | 2       | 2       | 4       | 3       | 3      | 1     | 1     |
| <i>Vertigo genesii</i> Gredler             | 1       | —       | —       | —       | —       | —       | —       | —       | —       | —      | —     | —     |
| <i>Vertigo geyeri</i> Lindholm             | —       | —       | 1       | —       | —       | —       | —       | —       | —       | —      | —     | —     |
| <i>Leiostryla anglica</i> (Wood)           | 1       | 4       | 5       | 5       | 3       | 8       | 13      | 15      | 11      | 17     | 5     | 2     |
| <i>Lauria cylindracea</i> (da Costa)       | 1       | 6       | 1       | 1       | 11      | 3       | 12      | 4       | 9       | 14     | 10    | 4     |
| <i>Vallonia pulchella</i> (Müller)         | —       | 1       | 2       | —       | —       | —       | —       | —       | —       | —      | —     | —     |
| <i>Acanthinula aculeata</i> (Müller)       | 2       | 6       | 3       | 3       | 6       | 7       | 6       | 11      | 8       | 12     | 9     | 2     |
| <i>Spermodea lamellata</i> (Jeffreys)      | —       | 7       | 3       | 7       | 8       | 12      | 11      | 16      | 15      | 21     | 6     | 3     |
| <i>Ena obscura</i> (Müller)                | —       | —       | —       | 1       | —       | 1       | —       | —       | 1       | —      | —     | —     |
| <i>Punctum pygmaeum</i> (Draparnaud)       | 1       | 2       | 3       | 4       | 7       | 7       | 3       | 11      | 13      | 5      | 4     | 1     |
| <i>Discus rotundatus</i> (Müller)          | 3       | 29      | 15      | 27      | 19      | 35      | 31      | 31      | 50      | 44     | 19    | 18    |
| <i>Vitrina pellucida</i> (Müller)          | —       | —       | —       | —       | —       | —       | —       | 1       | —       | 1      | —     | —     |
| <i>Vitrea contracta</i> (Westerlund)       | 1       | 8       | 6       | 12      | 27      | 33      | 28      | 28      | 30      | 24     | 14    | 3     |
| <i>Nesovitrea hammonis</i> (Ström)         | —       | 1       | —       | 3       | 2       | 1       | 1       | —       | 2       | 1      | 1     | 1     |
| <i>Aegopinella pura</i> (Alder)            | 1       | 5       | 2       | 5       | 7       | 11      | 10      | 14      | 18      | 8      | 12    | 6     |
| <i>Aegopinella nitidula</i> (Draparnaud)   | 4       | 15      | 8       | 9       | 13      | 12      | 20      | 12      | 15      | 29     | 13    | 8     |
| <i>Oxychilus cellarius</i> (Müller)        | 1       | 3       | 5       | 9       | 6       | 8       | 9       | 8       | 13      | 9      | 6     | 2     |
| <i>Oxychilus alliarius</i> (Miller)        | —       | —       | 1       | 1       | —       | 1       | —       | —       | —       | —      | —     | —     |
| <i>Zonitoides excavatus</i> (Alder)        | —       | —       | —       | —       | 1       | 2       | 1       | 1       | 1       | —      | —     | —     |
| <i>Zonitoides nitidus</i> (Müller)         | 1       | —       | 3       | 2       | 2       | 1       | —       | 4       | 2       | 1      | 1     | —     |
| Limacid plates                             | —       | 4       | 6       | 6       | 4       | 2       | 5       | 4       | 10      | 4      | 3     | —     |
| <i>Euconulus fulvus</i> (Müller)           | 1       | 6       | 3       | 4       | 6       | 4       | 7       | 5       | 8       | 14     | 4     | 2     |
| <i>Clausilia bidentata</i> (Ström)         | 1       | 2       | 1       | 2       | 1       | 3       | 2       | 2       | 1       | 1      | —     | 1     |
| <i>Balea perversa</i> (Linné)              | —       | 3       | 3       | 4       | 5       | 3       | 7       | 3       | 8       | 11     | 7     | 3     |
| <i>Trichia hispida</i> (Linné)             | —       | 1       | —       | —       | 5       | 1       | 3       | 3       | 1       | 3      | 1     | 2     |
| <i>Arianta arbustorum</i> (Linné)          | —       | +       | —       | —       | +       | —       | —       | +       | —       | +      | +     | +     |
| <i>Cepaea/Arianta</i>                      | —       | 2       | 3       | 1       | 8       | 4       | 2       | 3       | 2       | 2      | 2     | 1     |
| <i>Cepaea</i> spp.                         | —       | —       | +       | +       | +       | +       | +       | —       | —       | +      | —     | —     |
| <i>Pisidium amnicum</i> (Müller)           | —       | —       | —       | —       | —       | —       | —       | —       | —       | 1      | —     | —     |
| <i>Pisidium casertanum</i> (Poli)          | 4       | 47      | 19      | 30      | 67      | 69      | 111     | 154     | 188     | 139    | 87    | 102   |
| <i>Pisidium personatum</i> Malm            | 2       | —       | —       | 1       | 2       | 5       | 7       | 5       | 11      | 12     | 10    | 3     |
| <i>Pisidium milium</i> Held                | 1       | 3       | —       | 1       | 1       | 4       | 3       | 8       | 2       | —      | 2     | 1     |
| <i>Pisidium subtruncatum</i> Malm          | —       | 8       | 5       | 3       | 4       | 7       | 6       | 9       | 10      | 14     | 12    | 13    |
| <i>Pisidium hibernicum</i> Westerlund      | —       | 1       | —       | —       | —       | —       | —       | —       | —       | —      | —     | —     |
| <i>Pisidium tenuilineatum</i> Stelfox      | 2       | 12      | 20      | 16      | 31      | 52      | 31      | 56      | 51      | 55     | 56    | 32    |

N.B. *Pisidium* totals refer to the number of individual valves.



MOLLUSCA

Shells were found only in the calcareous tufa. Their preservation was generally very good although some specimens from the upper samples were rather corroded.

The deposit is very much richer than the earlier accounts suggest. The list of species known has been doubled. The systematic sampling through the tufa revealed little change in the composition of the fauna. However *Vertigo genesii*, *Vertigo geyeri* and *Succinea oblonga* (the last also recorded by Forbes) were only detected in the basal samples and in very low numbers. The occurrence of these, which are characteristic of the Late-glacial or earliest Post-glacial, is puzzling and out of character with the assemblage as a whole. These basal samples may perhaps contain material that has survived from a much earlier phase of accumulation; Bristow (1862, Fig. 72) illustrates disturbances at this horizon suggestive of frost involutions.

*Vallonia costata* and *Vitrea crystallina* were not recovered from the sampling column but were detected only in a spot sample taken from the lower half of the deposit.

The presence of flowing water is suggested by the nodular lithology at the base of the tufa and the abundance of *Pisidium*. Seven species of *Pisidium* are now known including *Pisidium amnicum*, *P. milium*, *P. subtruncatum*, *P. hibernicum* and *P. tenuilineatum*. *P. amnicum* is especially characteristic of slow flowing streams. The published accounts of sand and clay seams interstratified with tufa also suggest stream action.

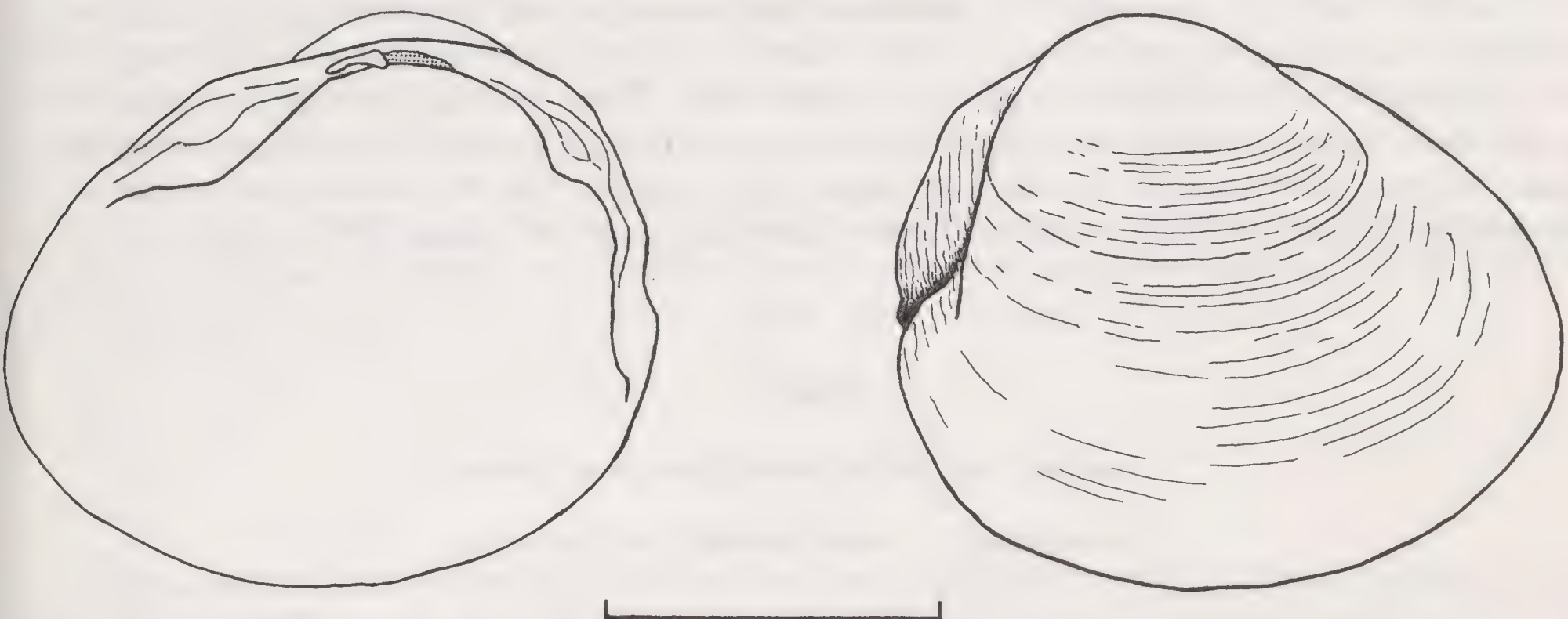


Fig. 3. Right valve of *Pisidium tenuilineatum* showing posterior distortion. Scale bar represents 1 mm.

The occurrence of *Pisidium tenuilineatum* is noteworthy. Early British accounts of the ecology of this species suggest that it is restricted to canals or sizeable rivers. On the Continent, however, it is also known to live in lakes and even a shallow karstic mere (Ložek, 1956). Recently it has been found in a lake in Sussex (Kerney, 1970). In such environments the shell is thinner and more delicate with less robust hinge-plate and hinge-teeth and it is apparent that the type described by Stelfox (1918) is an abnormally thickened riverine form (var. *typica* Odhner) analogous to the var. *ponderosa* of *P. casertanum* and the var. *crassa* of *P. nitidum*. The fossil shells from Totland, together with those from calcareous tufas of comparable age at Brook (Kerney *et al.*, 1964) and Folkestone (Kerney *et al.*, in preparation), are mostly of this thin-shelled form (var. *alpina* Odhner). A further curious feature of the Totland shells is the fact that about half the population is badly distorted at the posterior end (Fig. 3), suggestive of parasitism. Only *P. tenuilineatum* was affected at Totland although occasional examples of this phenomenon have been observed in other species elsewhere.



The only other freshwater species found was *Lymnaea truncatula*, a species characteristic of damp ground. The earlier records of *Unio* and *Planorbis* need checking; they could well be derived fossils from the underlying Headon Beds. Such shells were detected in the basal samples of the present sequence, but were clearly Tertiary forms.

The general nature of the land mollusc fauna is one of a closed forest. The environment was clearly shaded as well as wet. *Spermodea lamellata* and *Leiostryla anglica* are present throughout, together with *Discus rotundatus*, *Oxychilus cellarius*, *Vertigo pusilla*, *V. substriata* and *V. moulinsiana*. *Balea perversa* was quite common and *Zonitoides excavatus* was an unexpected discovery in a calcareous context. A sinistral example of *Lauria cylindracea* was also detected (90–95 cm).

*Pupilla muscorum* is listed by Kennard and Warren (1904), but this species was not found during the present study. An examination of Kennard's material in the British Museum (Natural History) showed that many of his "muscorum" were in fact juvenile *Leiostryla anglica*. There were some true *Pupilla*, but judging from the matrix filling the apertures, they apparently did not come from the tufa but presumably from some overlying hillwash.

There is now a voluminous literature on the banding polymorphism of *Cepaea* and the factors and selection pressures that govern it, both at the present day and at various times in the past. This has been the subject of two exhaustive studies by Currey and Cain (1968) and Cain (1971), who have examined a large number of sites in southern Britain. It is therefore interesting to comment on the differences between the morph frequencies of fossil *Cepaea* from the Totland tufa and the populations living on this site. The results are given in Table 2 and can be summarized thus: (a) that all the *C. nemoralis* from the tufa were unbanded; (b) no living *C. nemoralis* could be found on the site; (c) all the fossil *C. hortensis* were five-banded, although both this morph and the unbanded morph were found living. These findings endorse those discussed in the above papers, namely that there has been a contraction in the distributional range of *C. nemoralis* since the cessation of tufa formation, and secondly that the unbanded morph of *C. nemoralis* is apparently commoner in 'hotter times and regions' (Cain, 1971).

TABLE 2

Fossil and modern samples of *Cepaea* from Totland

0 = unbanded, 3 = mid-banded, 5 = five-banded

|                         |        | 0  | 3 | 5  | total |
|-------------------------|--------|----|---|----|-------|
| <i>Cepaea nemoralis</i> | fossil | 11 | — | —  | 11    |
| <i>Cepaea nemoralis</i> | modern | —  | — | —  | —     |
| <i>Cepaea hortensis</i> | fossil | —  | — | 6  | 6     |
| <i>Cepaea hortensis</i> | modern | 13 | — | 12 | 25    |

#### OTHER FOSSILS

Ostracod valves were common (Fig. 4) and could all be referred to one species, *Ilyodromas olivaceus* (Brady and Norman). This is a crawling form and is characteristic of springs.

A further fossil that seems to be diagnostic of spring-tufa environments is a minute *Dentalium*-like tube about 3.5 mm in length. Occasional examples were recovered throughout the tufa but they cannot be specifically named although they probably belong to a small species of caddis.

The only other fossils recovered were the seeds of *Eupatorium cannabinum* L. (hemp agrimony) which again occurred throughout the deposit (actual numbers given in Preece, 1978). The semi-aquatic habitat of this species together with its resistant seed coat undoubtedly favour its preservation.



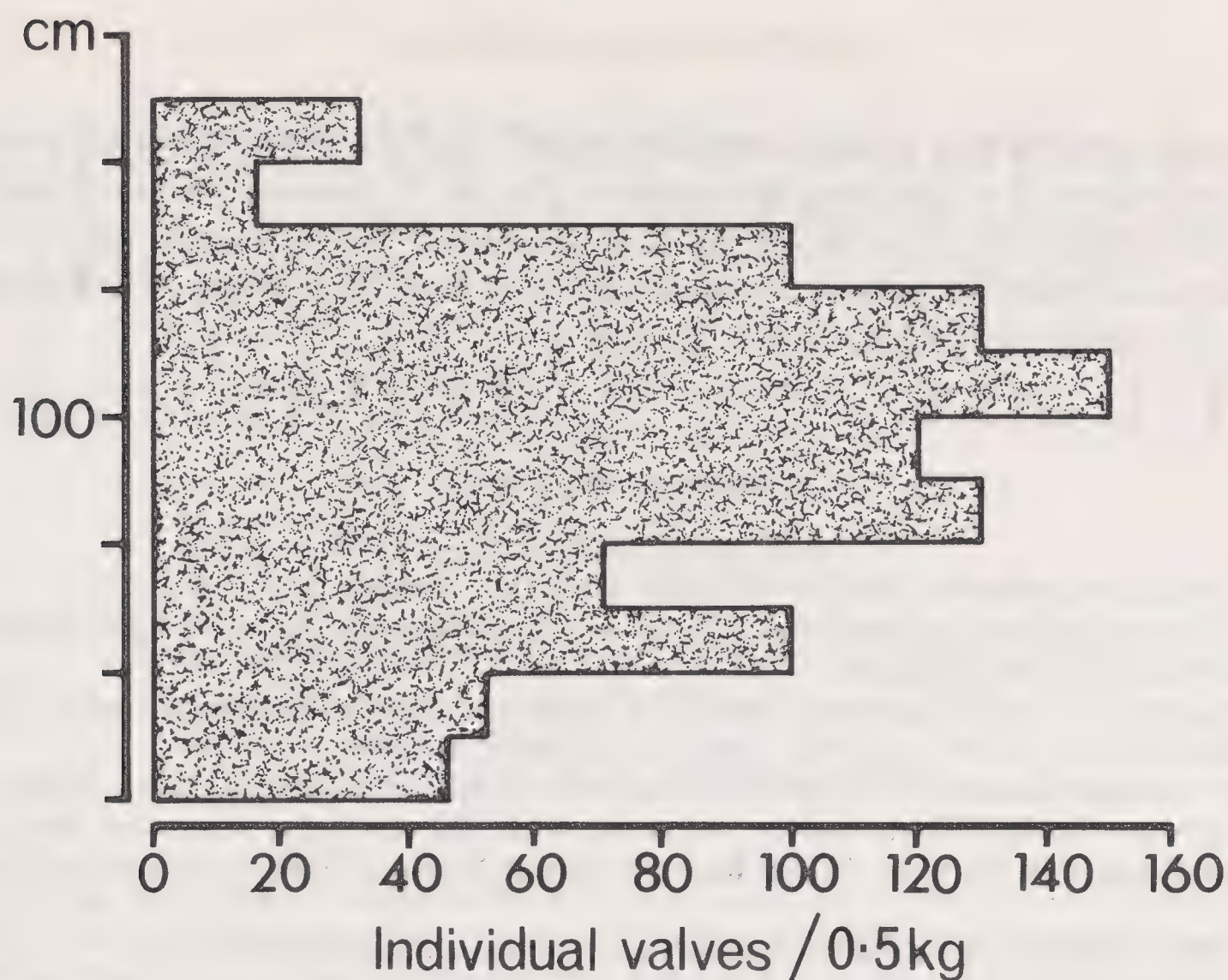


Fig. 4. Absolute frequencies of the ostracod *Ilyodromas olivaceus* (Brady and Norman).

Two organic lenses, sampled by I. J. Killeen in 1969, were analysed for pollen by Dr. C. Turner. The material proved too oxidized for adequate pollen preservation although isolated grains of the following were seen: *Pinus*, *Ulmus*, *Alnus*, Gramineae, Compositae.

### CONCLUSIONS

The increased knowledge of the fauna does not support Bristow's contention that the tufa formed in a small lake or pond but amply confirms Kennard and Warren's conclusion that the depositional environment was 'a damp land-surface, over which oozed the water, highly charged with carbonate of lime, which was thrown out of the Headon Hill limestones by springs'. The cessation of tufa formation has been attributed to the tapping of springs as the result of cliff recession (Reid and Strahan, 1889).

A series of molluscan assemblage zones has recently been proposed based on evidence derived from rather longer sequences in southern Britain (Kerney, 1977; Preece, 1978). The type locality for these zones is Folkestone in Kent (Kerney, Preece and Turner, in preparation). The molluscan fauna from Totland, which is rich in *Spermodea lamellata* and *Leiostyla anglica*, belongs to sub-zone d<sub>2</sub>. Three radiocarbon dates have been obtained from this zone: 7500 ± 100 BP. (St-3410) from Folkestone (Kerney, Preece and Turner, in preparation); 6730 ± 150 BP. (Q-1343) from Blue Anchor Bay, Somerset (Kerney, 1976); 6260 ± 120 BP. (Q-1533) from Ddôl, Flintshire (Preece, 1978). Many more dates are needed, however, to establish the time span of this assemblage in different parts of southern Britain.

It was not possible to obtain a pollen spectrum from Totland but at Folkestone and Blue Anchor Bay, zone d assemblages are associated with pollen zones VIc/VIIa (Late Boreal/Atlantic).



## ACKNOWLEDGEMENTS

This work was carried out while in receipt of a N.E.R.C. research studentship which is gratefully acknowledged. I would also like to thank Dr. M. P. Kerney for checking the *Pisidium* and for useful discussion. Dr. Eric Robinson kindly named the ostracods and Dr. C. Turner examined the organic lenses for pollen. I am also grateful to M. J. Willing for his help and Dr. C. R. C. Paul for checking the *Columella*.

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MORPHOLOGY OF THE OVIPAROUS ROUGH  
WINKLE, *LITTORINA ARCANNA* Hannaford Ellis,  
1978, WITH NOTES ON THE TAXONOMY OF THE  
*L. SAXATILIS* SPECIES—COMPLEX  
(PROSOBRANCHIA: LITTORINIDAE).

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(Read before the Society, 16 December, 1978)

*Abstract:* *Littorina arcana* is an oviparous species which is often collected with the related but ovoviviparous *L. rudis*, both species occurring apparently in the same zone on many British beaches. The shells of the two species are frequently indistinguishable and since the species are sympatric they cannot be reliably separated in the field.

Dissection of freshly killed animals and identification from the characteristics of the pallial oviduct and the ciliated field (which lies between the genital tract and the columellar muscle) is the only sure way to separate these two species. The ciliated field of *L. arcana* is comparatively small and inconspicuous. The pallial oviduct is distinguished by the relatively large so-called albumen and capsule glands and the development of a jelly gland in a position homologous to the brood pouch in *L. rudis*. The penis of *L. arcana* is typically relatively shorter, has more penial glands, a tapering tip and is often almost triangular in shape. However, these penial differences are not diagnostic. The shell is often patulous in character but many other shell varieties can be produced.

Circumstantial evidence suggests that the report of oviparity in rough winkles by Seshappa (1947) was based on observation of *L. arcana*, rather than the other oviparous rough winkle, *L. nigrolineata*. Facts that suggest that the description of *L. patula* given by Heller (1975) was based on a mixture of specimens of *L. arcana* and *L. rudis* are considered, and a revision of the taxonomy of the rough winkles is proposed whereby the name *L. patula* is regarded as synonymous with *L. rudis*.

*L. arcana* appears to be a widespread species, so far, known to occur in Eire, France, Norway and Britain.

In a previous paper (Hannaford Ellis, 1978) a new species of rough winkle, *L. arcana*, was diagnosed. The present paper describes the morphology of this species in greater detail, comparing it with the morphology of the closely related and sympatric species *L. rudis* (Maton, 1797) and *L. nigrolineata* Gray (1839), and also revises the taxonomy of the 'saxatilis' species—group to which *L. arcana* belongs.

In the field *L. arcana* is likely to be confused most often with *L. rudis* because of the similarity of their shells and their habitat. Anatomically however, these two species are quite distinct and these distinctions are described in detail to aid the identification of *L. arcana*.

The females of *rudis* and *arcana* proved distinguishable by their pallial oviduct structure. *L. arcana* is oviparous and has the large albumen and capsule glands and the jelly gland which are typically seen in oviparous species. Indeed it was through its oviparity expressed in its oviduct and also the production of egg masses that the existence of this new species first came to notice. In contrast, *L. rudis* is ovoviviparous and the oviduct structure differs in that the albumen and capsule glands are relatively small and a brood pouch replaces the jelly gland.

Though the females were easy to identify, the males of these species were initially difficult to separate for two reasons. Firstly, comparison of the shells of the oviparous (*L. arcana*) females with those of the ovoviviparous (*L. rudis*) females did not reveal any consistent distinctive differences which might then be applied to separate the associated males into species. In this respect *L. arcana* proved to be unlike *L. nigrolineata* and *L. neglecta* (Bean, 1844); both these



species have distinctive shell types which has proved useful in specific characterization. Secondly, there were no distinctive types of penial shape amongst the associated males. The forms of the penes were very variable and seemed to be continuously variable. This is surprising since in the case of the two flat-winkle species, *L. obtusata* (L.) and *L. mariae* Sacchi and Rastelli, 1966 (the shells of which are so similar that until 1966 they were considered to be one species) the specific difference in the form of the penis is striking, and is probably of importance in species recognition.

However, with the later discovery of a species-marker independent of sex, shell or penis, it proved possible to separate the males decisively into one species or the other. This marker was a ciliated field on the mantle which differed, particularly in extent, in the two species. The diagnostic differences were confirmed initially with the location of a pure population of *L. arcana* at Dunbar in Scotland. Subsequently, in Anglesey, they were found to be reliable at those sites where local differences in shell characteristics of *L. arcana* and *L. rudis* were unequivocal and the shell could be used as a species-marker. The character of the ciliated field was then used to identify and separate males of *L. arcana* and *L. rudis* and typical (but not diagnostic) differences which occur in penis structure were identified.

The discovery of the existence of *L. arcana* has proved to be of more consequence in the taxonomy of the *L. saxatilis* species-complex than simply the addition of a new species to those already known. For reasons that are discussed at the end of this paper, it is thought that one of the four species previously recognized by Heller (1975), *L. patula* Thorpe, 1844, was probably described from a mixture of patulous-shelled specimens of *L. rudis* and *L. arcana*. Hence a revision of the taxonomy of the group was necessary.

## COMPARATIVE MORPHOLOGY

I. *The ciliated field.* In *L. rudis*, *L. nigrolineata* and *L. arcana* there is a localized pad of densely ciliated tissue, the ciliated field (CF) which is an elaboration of the epithelium of the inner mantle wall. Both the position and the extent of the CF are important diagnostic characters. The field lies between the prostate and the columellar muscle in the males and, in an analogous position, between the oviduct and the columellar muscle in the females.

The CF is only readily apparent in animals freshly killed (by briefly boiling them) since usually it is pink and stands out against the white or black of surrounding mantle tissues. In preservation it loses its colour and it can be difficult to trace its true extent. It should be noticed that in the males, because the prostate is similarly pink, the CF appears to be an extension of this gland.

Histological examination shows that the tissue is composed of columnar, densely ciliated, epithelial cells with a few scattered goblet cells (see Plate 1). The function of this tissue and the significance of its variation in position and extent in different species are not known. Its existence as such seems not to have been previously recorded.

### (I,i) Ciliated field and prostate characters in male *L. arcana* and *L. rudis*

In order to examine the ciliated field it is necessary to open the mantle cavity.

In *L. rudis* males the CF is comparatively extensive and lies adjacent to the distal end of the prostate (Fig. 1A). The prostate is comparatively long and usually smooth, being only slightly elaborated with transverse folds. Because of the position and extent of the CF the termination of the prostate folds is often seen to lie well forward of, or below, the anus, acting to direct sperm round the CF into the seminal groove of the penis.

In *L. arcana* males (Fig. 1B) the CF is generally inconspicuous, usually forming a narrow band (less than the depth of the prostate) beside the ventral edge of the prostate. The prostate gland is comparatively short, usually with marked transverse folds. The distal termination of the



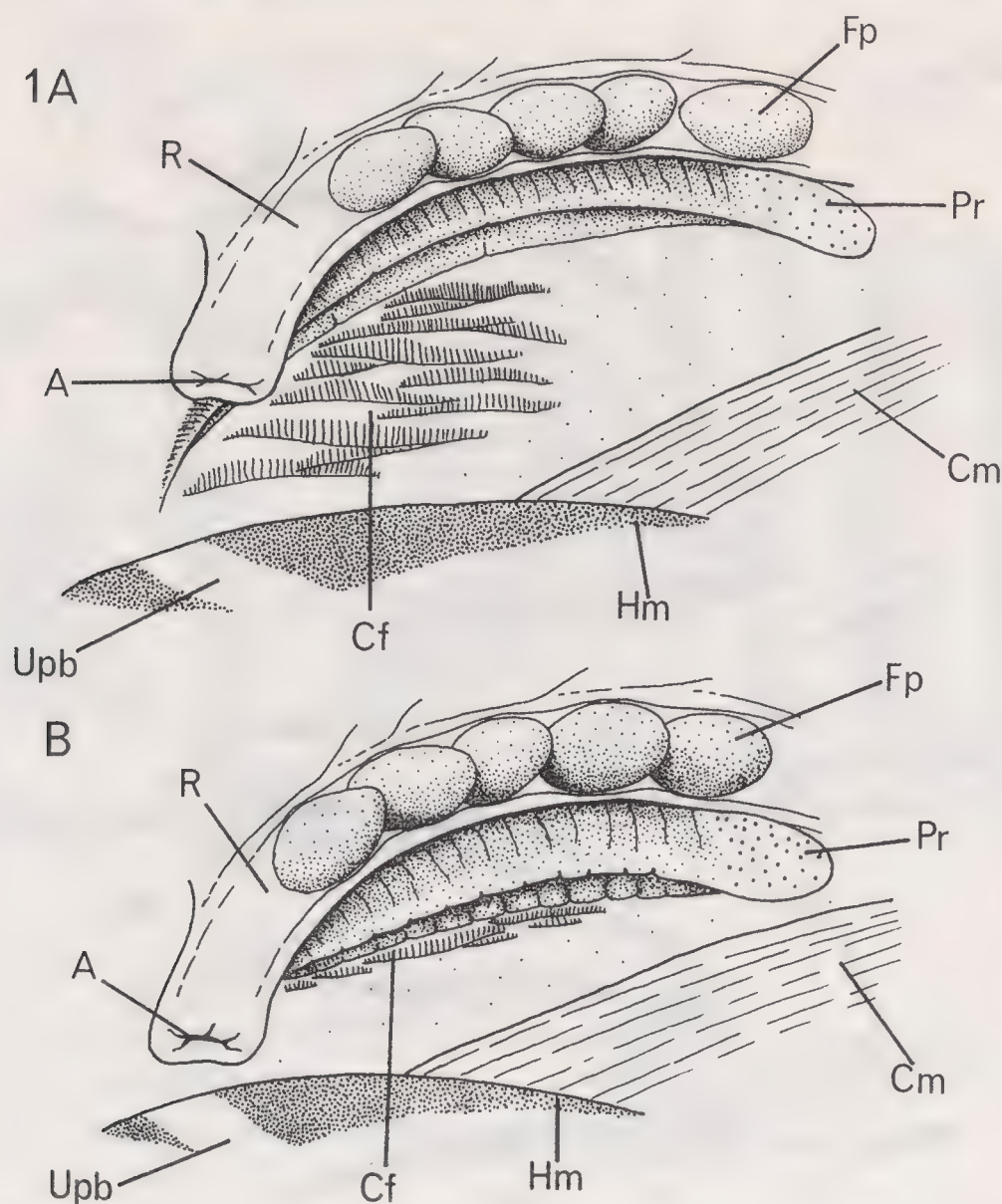


Fig. 1. Ciliated field and prostate characters. A) *L. rudis* B) *L. arcana*. A:-anus. Cf:-ciliated field. Cm:-columnellar muscle. Fp:- faecal pellet. Hm:- head mass. Pr:- prostate, (large dots = translucent section). R:- rectum. Upb:- unpigmented band.

prostate folds is not often apparent unless the anus and rectum are reflexed.

This marked difference, particularly in extent, of the CF has been seen in all the British specimens of *L. rudis* and *L. arcana* I have examined. However, a sample sent live from America by E. V. Scott contained a small number of *L. rudis* the ciliated fields of which were small and very *arcana*-like. Interestingly, there were no *L. arcana* in this sample. It may be that this species does not occur on the eastern seaboard of the U.S.A., and the characteristics of *rudis* are correspondingly less accentuated. It seems therefore that though the character of the CF appears to be reliable for British specimens it might not apply in other parts of the world.

In all the rough winkle species the prostate has two segregated types of secretory cell. The proximal secretory cells appear translucent in freshly killed animals. When sectioned and stained with modified Mallory-Heidenhain stain (Cason, 1950) these cells have many round blue-stained packets of secretory product. The distal section, which is the greater part of the prostate, appears opaque in freshly killed animals and the secretory products of these cells are irregularly shaped bodies which stain orange. The chemical nature of the secretory products is unknown.

The differences in extent of the CF and transverse folding can frequently be seen externally (Plate 1 and Fig. 8). However external appearances can be misleading, e.g. if the CF is folded into the mantle cavity, and dissection is necessary for precise identifications.

The character of the CF is independent of that of the penis and is apparent in males without penes (through shedding or parasitic castration) and in males without fully developed penes. It is crucial in identifying and separating males of these species as they can be confused on penial morphology. Males of the other related taxa can be reliably distinguished on shell and penis characteristics (Heller, 1975).



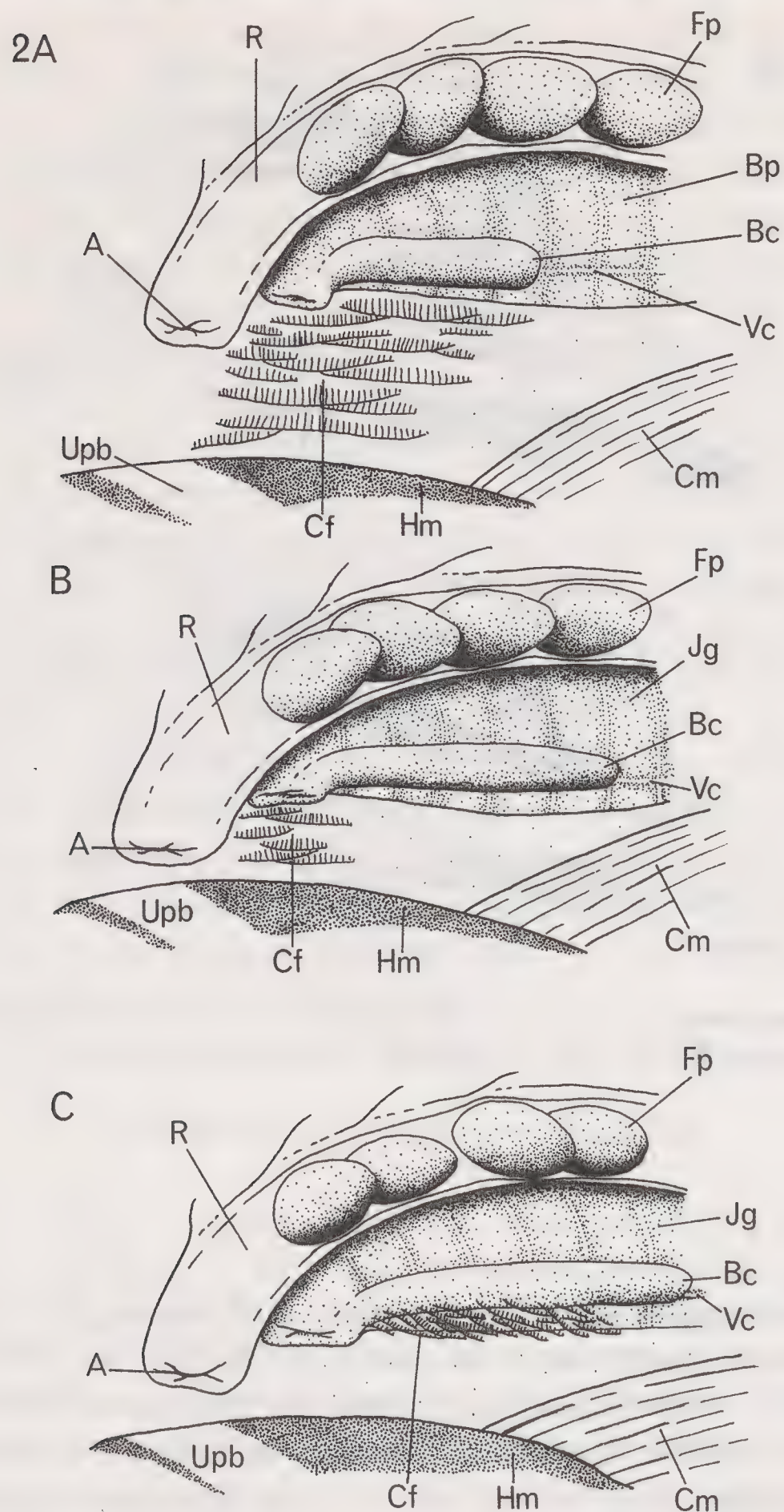


Fig. 2. Ciliated field position and extent in female. A) *L. rudis* B) *L. nigrolineata* C) *L. arcana*. As in Fig. 1 also Bc:- bursa copulatrix. Bp:- brood pouch. Jg:- jelly gland. Vc:- ventral channel.

(I,ii) Ciliated field characters in females of *L. rudis*, *L. arcana* and *L. nigrolineata*

The CF in female *L. rudis*, like that in the male is very extensive and is frequently thrown into folds (Fig. 2A, Plate 2). In *L. nigrolineata* the CF is also often heavily folded but of much smaller extent and positioned near the opening of the oviduct (Fig. 2B). In *L. arcana* the CF is also small relative to that of *L. rudis*, but rarely exhibits folds, usually being an almost flat sheet of tissue. Often it includes a small part of the mantle covering the jelly gland (Fig. 2C). As in the males, the CF is scarcely apparent externally, in this contrasting with the prominent CF of *L. rudis* (Plate 2, Fig. 9).

The extent of the CF can, of course, vary from individual to individual and also from population to population. For example in the *L. arcana* population at Porth Swtan, the CF is barely discernible in most specimens, whereas in *L. arcana* from Dunbar it is readily apparent although small.



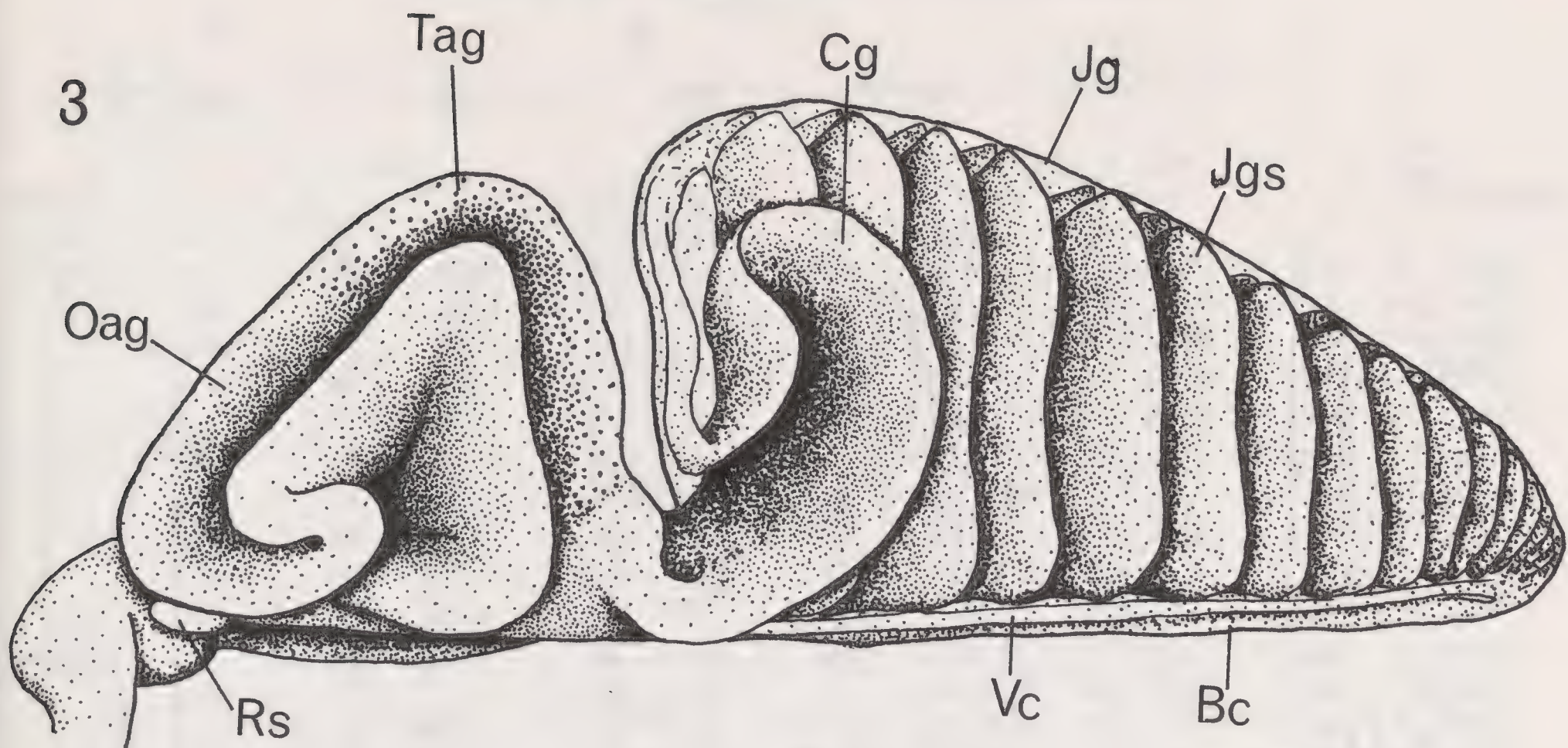


Fig. 3. Lateral view (right side) of the pallial oviduct of *L. arcana* (not fully mature). Bc:- bursa copulatrix. Cg:- capsule gland. Jg:- jelly gland. Jgs:- jelly gland septa. Oag:- opaque section of albumen gland. Rs:- receptaculum seminis. Tag:- translucent section of albumen gland. Vc:- ventral channel.

CF characters in females are helpful in confirming or making specific identifications of immature *L. rudis* and *L. arcana*. Immature *L. nigrolineata* females can be easily distinguished by their shells.

2. *Morphology of the pallial oviduct.* The structure of the pallial oviduct is similar in all the British oviparous species and is distinctly different from that seen in the ovoviviparous species. The comparison of pallial oviduct morphology between *L. arcana* and *L. rudis* illustrates the differences and is also useful in identifying these species.

The parts of the pallial oviduct are homologous in the two types. The initial part of the pallial oviduct is more or less tubular and, in the mature animal, the walls are highly glandular. This part is twisted into loops, the largest of which is not visible in lateral view, as it is overlain by subsequent loops of laterally flattened oviduct, known as the albumen gland (Linke, 1933; Sacchi, 1975). This is not one gland but several as can be determined histologically, and often visually. Proximally the albumen gland appears opaque in freshly killed animals and the cells of this part stain blue with modified Mallory-Heidenhain stain. Distally it appears translucent and the cells do not stain at all. In the mature state the lateral flattening of this part of the oviduct is not apparent because of the swollen, glandular nature of the walls which also makes it difficult to trace the path of the convolutions, since the walls of one part of the duct are closely applied to the walls of neighbouring convolutions. In places, though, parts of the lumen, appearing dark, can be seen through the walls of the oviduct, creating the illusion that it is the outer surface of part of the duct. These convolutions are succeeded by another laterally flattened loop, which is known as the capsule gland, and stains red with modified Mallory-Heidenhain stain. It overlies the distal section of the oviduct which has a complex of incomplete septa extending into the lumen.

In *L. arcana* the proximal convolutions are relatively large (see Plate 2 and Figs. 3 and 9) and in the mature condition the septa of the distal section are fleshy, and completely fill the lumen. These glandular septa are thought to secrete the jelly matrix of the egg mass and so this distal section is known as the jelly gland. The overall appearance of the mature oviduct, *in situ*, is of a large whitish mass, the structure of which is often barely discernible. The path of the



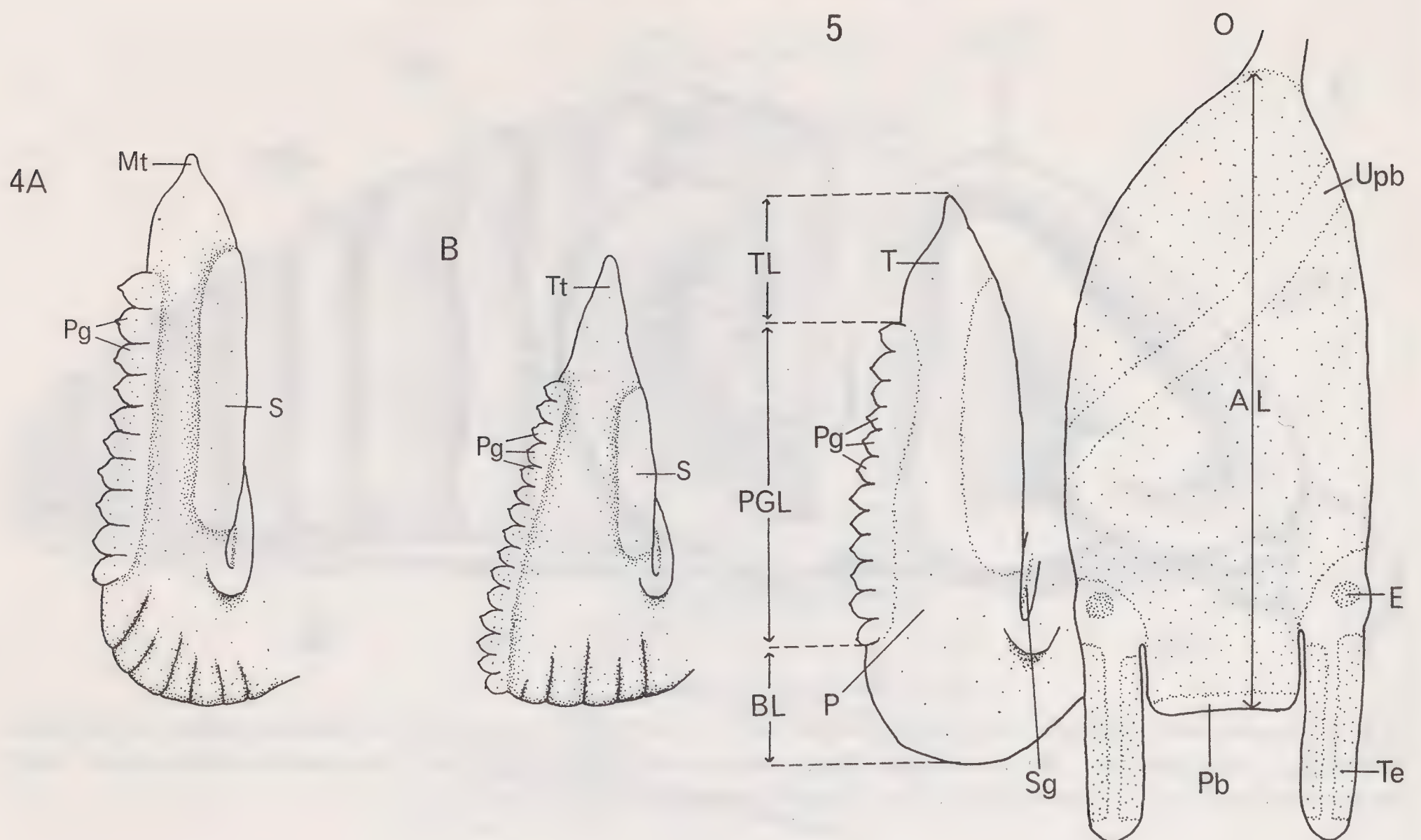


Fig. 4. Dorsal view of penis. A) typical "*rudis*" shape. B) typical "*arcana*" shape. Mt:- mucronate tip. Pg:- penial glands. S:- swelling. Tt:- tapering tip.

Fig. 5. Measurements used. AL = Length of head mass. BL = base length. PGL = length of penial gland zone. TL = length of tip. PL = BL + PGL + TL. E:- eye. O:- oesophagus. P:- penis. Pb:- proboscis. Pg:- penial gland. Sg:- sperm groove. T:- tip. Te:- tentacle. Upb:- unpigmented band.

convolutions is easiest to see in immature oviducts before the walls become highly glandular (see Fig. 3).

In *L. rudis* the proximal convolutions are small relative to the overall size of the oviduct and the septa of the distal section do not become fleshy with maturity. Instead, developing embryos fill the lumen; hence the distal section is known as the brood pouch.

Since in immature females of *L. arcana* and *L. rudis* the distal section is neither fleshy nor packed with developing spat, it is the difference in the proportions of the parts of the oviduct which is useful in identifying young specimens and, with the character of the CF, is reliable for the separation and identification of immature females. Young females of other related taxa can be reliably identified on the character of the shell.

**3. Penis morphology.** The range of variation of the penis morphology seen in *L. arcana* overlaps, to a limited extent, that observed in *L. rudis*. This makes it unreliable as a diagnostic feature of either species. Nevertheless it is possible to describe a typical '*rudis*'-shape of penis and a typical '*arcana*'-shape (Fig. 4).

Various measures of the penis have been taken from individuals of the two species collected from mixed populations at five sites. These measurements are defined in Fig. 5 and are used to give a quantitative comparison of the proportions of the penis in the two species in Table 1.

Strong bimodality is apparent in the lumped data for some aspects of penis shape, and the results of Mann-Whitney *U* tests are significant. But attention should also be paid to the fact that the data for the two species are continuous, i.e. the ranges of the ratios of penis shape for the two species overlap. Thus the penis shape is characteristic but not diagnostic.



TABLE 1

Comparison of penial shape characteristics of *L. arcana* with *L. rudis* using Mann-Whitney *U* test.

| Ratio  | Site | <i>L. arcana</i> |        |                       | <i>L. rudis</i> |        |                       | two-tailed |         |
|--------|------|------------------|--------|-----------------------|-----------------|--------|-----------------------|------------|---------|
|        |      | n                | median | range of observations | n               | median | range of observations | z          | p       |
| PL/AL  | P.S. | 86               | .886   | .650-1.275            | 100             | 1.120  | .776-1.333            | 9.39       | <.00006 |
|        | A.B. | 61               | .895   | .648-1.143            | 50              | 1.066  | .800-1.349            | 4.91       | <.00006 |
|        | B.R. | 68               | .922   | .712-1.156            | 72              | 1.091  | .810-1.346            | 6.89       | <.00006 |
|        | Y.W. | 60               | .821   | .683-1.014            | 40              | 1.061  | .840-1.324            | 7.79       | <.00006 |
|        | D.   | 37               | .867   | .613-1.137            | 32              | 1.071  | .877-1.500            | 5.58       | <.00006 |
| TL/PL  | P.S. | 84               | .241   | .155-.388             | 94              | .235   | .134-.365             | 2.72       | .0066   |
|        | A.B. | 61               | .240   | .172-.321             | 49              | .250   | .147-.352             | .78        | .4354   |
|        | B.R. | 79               | .222   | .150-.381             | 73              | .242   | .159-.386             | 2.78       | .0054   |
|        | Y.W. | 60               | .250   | .143-.353             | 41              | .244   | .145-.347             | .23        | .8180   |
|        | D.   | 49               | .241   | .154-.362             | 34              | .239   | .169-.349             | .84        | .4010   |
| PGL/PL | P.S. | 89               | .735   | .529-.823             | 95              | .606   | .375-.780             | 9.38       | <.00006 |
|        | A.B. | 61               | .716   | .580-.815             | 50              | .600   | .448-.740             | 6.48       | <.00006 |
|        | B.R. | 79               | .723   | .455-.875             | 73              | .603   | .292-.726             | 8.46       | <.00006 |
|        | Y.W. | 60               | .732   | .600-.831             | 41              | .577   | .418-.744             | 7.83       | <.00006 |
|        | D.   | 47               | .729   | .571-.821             | 35              | .576   | .241-.733             | 6.73       | <.00006 |
| BL/PL  | P.S. | 91               | .000   | .000-.2352            | 93              | .1711  | .000-.3750            | 10.31      | <.00006 |
|        | A.B. | 61               | .0395  | .000-.1695            | 49              | .1408  | .000-.3529            | 6.47       | <.00006 |
|        | B.R. | 79               | .0333  | .000-.2860            | 72              | .1714  | .000-.3750            | 7.34       | <.00006 |
|        | Y.W. | 60               | .000   | .000-.1600            | 41              | .1710  | .012-.3890            | 7.93       | <.00006 |
|        | D.   | 48               | .0385  | .000-.1224            | 33              | .1429  | .0706-.4684           | 7.06       | <.00006 |

Sites:- P.S.:- Porth Swtan; A.B.:- Abraham's Bosom; B.R.:- Bell Rock; Y.W.:- Ynys Wellt; D.:- Dunbar

Measurements:- A.L.:- length of head mass; B.L.:- base length; P.G.L.:- length of penial gland zone; L.:- length of penis; T.L.:- tip length

Typically the penes of *L. arcana* are shorter relative to the size of the animal, than in the related taxa, *L. rudis* and *L. nigrolineata*. The tip, like that of *L. rudis* (and in contrast to that of *L. nigrolineata*), is fairly long, accounting for about a quarter of the total length of the penis in both species. Using the lumped data from the five sites considered, (the data from each site all show similar features) the penial glands range in number from 6-34 and may be arranged in a single row, or irregularly, or in a double row (4 or more penial glands in a row parallel to the main row) the proportion in each category being respectively 3:11:2. In *L. rudis* the range in number of penial glands is 4-26 and the proportion of each pattern of arrangement is 47:47:1. Thus all arrangements are seen in both species but in very different frequencies of occurrence. Fig. 6, A and B indicates the degree of overlap in this character. Very rarely, and only in *L. arcana* have triple rows of penial glands been seen. In *L. arcana* it is common for the penial glands to extend round the basal curve of the penis; this occurs in about two in every five cases, whereas in *L. rudis* it only occurred four times in 288 cases.

It is noticeable that the penis tip of *L. rudis* is frequently mucronate. This never occurs in *L. arcana* in which the tip tapers to a point. It is possible that this is important in species recognition. That it is not always readily apparent in penes of *L. rudis* could be due to the killing technique affecting the contraction of particular muscles.

At some sites the populations of *L. rudis* and *L. arcana* show specific differences in surface pigmentation of the penis. Pigmentation of *L. arcana* penes is usually confined to the sperm groove, whereas *L. rudis* penes rarely have pigmented sperm grooves but frequently have pigmented dorsal surfaces, the pigment being mainly limited to the basal area but extending towards the tip between the penial glands and the swelling on the head-mass side of the penis, typically covering a roughly triangular area.



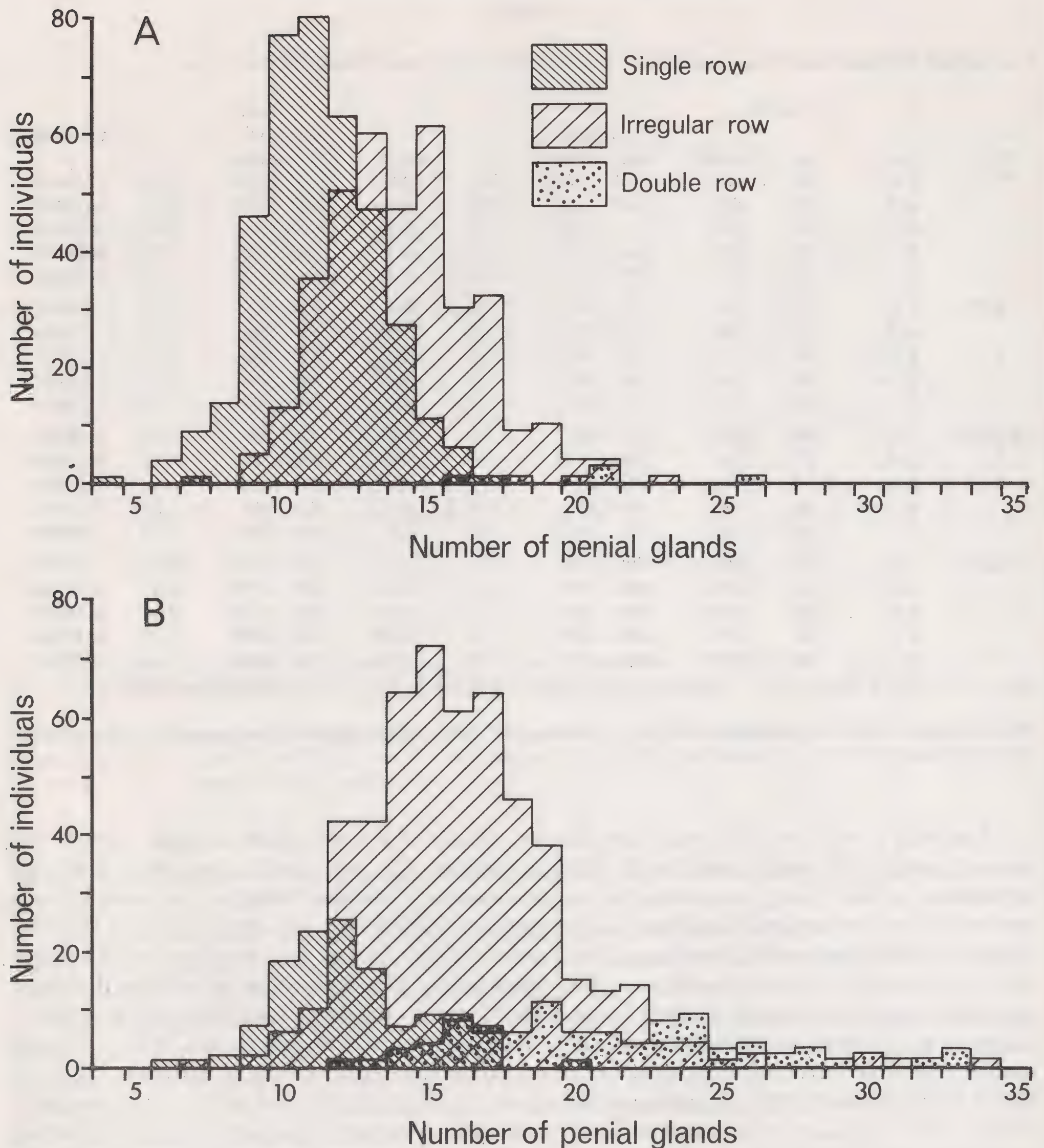


Fig. 6. Frequencies of patterns of arrangement of penial glands and number of penial glands. A) *L. rudis* B) *L. arcana*.

Identification of males of *L. arcana* should, of course, be based on the character of the CF and not on the penis.

4. *The shell.* The shell of *L. arcana* is very like that of *L. rudis* and is equally variable. There is no diagnostic character that distinguishes shells of this species from shells of *L. rudis* and no shell variety seems to be peculiar to one species or the other. Plate 3 shows the similarity of shells in the two species. All these shells were from the same randomly chosen sample. However, at many sites it is possible to find that a particular shell shape or colour is always associated with one or



other species. This can be of assistance to workers in the field who have previously identified these local differences. Some sites, such as Abraham's Bosom, Anglesey, have very distinctive local differences. Their shells of *L. rudis* are thick, smooth and orange and those of *L. arcana* are thin, heavily ridged and multicoloured with tessellations or bands. At other sites, such as Porth Swtan, the differences are much less marked and it is not possible to identify every animal on its shell. At many sites it is, however, noticeable that the shells of *L. arcana* exhibit, more strongly than those of *L. rudis*, patulous shell characteristics. The *patula* shell type is currently regarded (Heller, 1975) as exhibiting the characteristics described by Jeffreys (1865) i.e. short-spined, asymmetrical in spire view and with a wide, round aperture, showing little expansion and angulation below. The typical *rudis* shape is medium-spined, symmetrical in spire view and has an oval aperture considerably expanded and angulated below. These aspects of shell shape can be estimated respectively by the ratios shell height/shell width, shell diameter/shell width, internal mouth diameter/internal aperture length and internal aperture length/external aperture length (Fig. 7). Measurements were therefore made on shells of animals of both species collected from mixed populations at five localities and ratios were derived from these data to indicate the degree of expression of patulous characters in the two species at each locality.

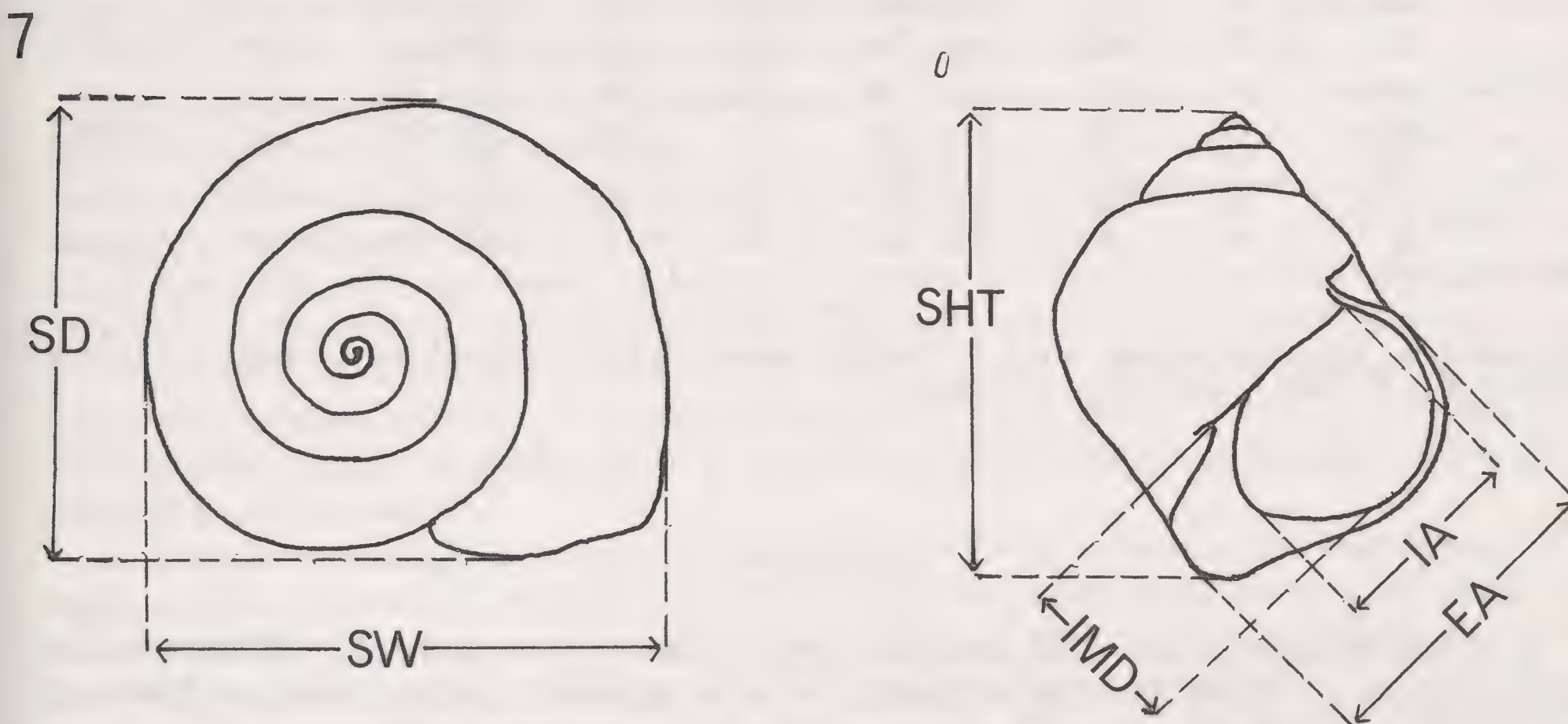


Fig. 7. Shell measurements used. EA:- external aperture. IA:- internal aperture. IMD:- internal mouth diameter. SD:- shell diameter. SHT:- shell height. SW:- shell width.

Comparisons between the ratios of the two species are given in Table 2 and it can be seen that shells of *L. arcana* are significantly more short-spined and asymmetrical than *L. rudis* at all sites. At four sites out of five the angulation and expansion of the lip is significantly less developed but only at one site are the shells of *L. arcana* more commonly rounder-mouthed than those of *L. rudis*. Overall the data confirm the suggestion that *L. arcana* is more strongly associated with the patulous shell shape than is *L. rudis*. Nevertheless both species can exhibit shells with either *rudis* or *patula* characteristics and as the overlap in ratios observed in the two species indicates, it is not possible to separate the species reliably by the shape of the shell.

#### EGG MASSES

In their early stages the eggs of *L. arcana* are usually rose-pink in colour, unlike those of the other oviparous winkles, the eggs of which are usually yellow. Typically the egg masses are laid in damp crevices near the top of the barnacle zone.



TABLE 2

Comparison of shell shape measurements of *L. arcana* with *L. rudis* using the Mann-Whitney *U* test.

| Ratio  | Site | <i>L. arcana</i> |        |                       | <i>L. rudis</i> |        |                       | two-tailed |         |
|--------|------|------------------|--------|-----------------------|-----------------|--------|-----------------------|------------|---------|
|        |      | n                | median | range of observations | n               | median | range of observations | z          | p       |
| SHT/SW | P.S. | 92               | 1.092  | .983-1.188            | 90              | 1.095  | 1.012-1.171           | 1.71       | .0872   |
|        | A.B. | 67               | 1.080  | 1.014-1.186           | 61              | 1.091  | 1.000-1.177           | 1.00       | .3174   |
|        | B.R. | 75               | 1.112  | 1.041-1.243           | 63              | 1.156  | 1.074-1.260           | 5.54       | <.00006 |
|        | Y.W. | 80               | 1.070  | .966-1.175            | 80              | 1.120  | 1.018-1.200           | 6.20       | .0046   |
|        | D.   | 73               | 1.080  | .955-1.183            | 68              | 1.099  | .959-1.230            | 2.84       | .0046   |
| SD/SW  | P.S. | 92               | .634   | .584-.677             | 90              | .664   | .610-.697             | 6.94       | <.00006 |
|        | A.B. | 67               | .608   | .574-.674             | 59              | .648   | .606-.708             | 7.13       | <.00006 |
|        | B.R. | 75               | .641   | .594-.689             | 63              | .667   | .626-.693             | 7.65       | <.00006 |
|        | Y.W. | 80               | .618   | .537-.699             | 80              | .661   | .610-.712             | 9.34       | <.00006 |
|        | D.   | 73               | .618   | .568-.690             | 68              | .653   | .586-.712             | 6.88       | <.00006 |
| IA/EA  | P.S. | 104              | .662   | .577-.832             | 87              | .661   | .568-.722             | .62        | .5352   |
|        | A.B. | 52               | .708   | .608-.798             | 56              | .651   | .580-.719             | 5.96       | <.00006 |
|        | B.R. | 75               | .632   | .576-.748             | 63              | .595   | .552-.648             | 6.87       | <.00006 |
|        | Y.W. | 50               | .636   | .595-.696             | 50              | .625   | .553-.650             | 3.07       | .00022  |
|        | D.   | 70               | .692   | .590-.795             | 69              | .644   | .569-.727             | 6.08       | <.00006 |
| IMD/IA | P.S. | 103              | .771   | .705-.859             | 85              | .781   | .687-.926             | 1.95       | .0512   |
|        | A.B. | 67               | .608   | .574-.674             | 59              | .648   | .606-.708             | 7.13       | <.00006 |
|        | B.R. | 74               | .787   | .714-.861             | 63              | .787   | .690-.855             | .11        | .9124   |
|        | Y.W. | 50               | .797   | .703-.878             | 50              | .782   | .714-.874             | 1.04       | .2984   |
|        | D.   | 70               | .780   | .680-.862             | 68              | .771   | .681-.878             | 1.32       | .1868   |

Sites:- (See Table 1)

Measurements:- E.A.:- external aperture; I.A.:- internal aperture; I.M.D.:- internal mouth diameter; S.D.:- shell diameter; S.H.T.:- shell height; S.W.:- shell width

## ECOLOGY

*L. arcana* seems to be more abundant on exposed shores where there are cliff faces or semi-permanent rocks, but it can also be found on more sheltered boulder beaches. The range extends from the *Verrucaria* zone into the top of the barnacle belt, thus occurring in the same zone as *L. rudis* and on some beaches replacing it. Where both occur together at Porth Swtan, its zonation in relation to *L. rudis* appears to vary with its reproductive activity. Work is still in progress on the complex nature of this zonation.

## DISCUSSION

The principal feature of *L. arcana* is its oviparity which immediately separates it from *L. rudis* as a distinct species. There are a few previous records of oviparity in rough winkles. Some are attributable to the closely related, but easily distinguished, oviparous species *L. nigrolineata*. However, there is one frequently quoted record by Seshappa (1947) which, although it has been attributed by both Sacchi (1975) and Heller (1975) to *L. nigrolineata*, should in my view be attributed to *L. arcana*. Seshappa reported oviparity from animals with shells 'found to agree very well both with the descriptions given by Alder for *L. rudissima* Bean and by Forbes and Hanley for *L. patula* Jeffreys'. [The original authority was C. Thorpe who gave, incorrectly, Jeffreys as the author.] Neither of these are shell varieties that I regard as synonymous with *L. nigrolineata*. His animals, too, laid pink egg masses in the aquarium. However, in a later paper



(1948), Seshappa had come to regard it as 'a case of the same species exhibiting both oviparous and viviparous [strictly, ovoviviparous] modes of reproduction,' probably because of the difficulty in separating the males corresponding with oviparous females from males of *L. rudis*, without the independent character of the ciliated field. Seshappa, consequently, did not raise his form to specific rank despite his earlier view that it 'should be regarded as quite distinct from the rest of the subspecies and varieties of *L. saxatilis*'.

The present taxonomy of the rough winkles was published by Heller in 1975. He considered that there were four species, *L. rudis*, *L. nigrolineata*, *L. neglecta* and *L. patula* which he described from differences in shell characters, penial characters, reproductive biology and zonation. Subsequently doubts have been expressed informally about the specific status of *L. patula* which many regard as an ecotype of *L. rudis*, indeed many of the characters described for *L. patula* fall within the range of variation of *L. rudis*. However my studies suggest that *L. patula* was described largely from specimens of *L. arcana*, mixed with some specimens of *L. rudis*. Several facts support this suggestion. Re-examination of Heller's material held at Liverpool University revealed a substantial number of *L. arcana* which must have been used in the evaluation of *L. rudis* and *L. patula*. Also, in 1977 specimens of *L. arcana* were sent to Dr. Heller. These he returned labelled *L. patula* in the cases of those with patulous shells and '*L. unknown*' for the remainder. It seems probable therefore that he based his initial division between *L. rudis* and *L. patula* on the shape of the shell. At many sites, for example Abraham's Bosom, where the shells of *L. arcana* are strikingly coloured and distinctly patulous there is an obvious division between shells of the '*patula*' type and shells of the '*rudis*' type. Since *L. arcana* is strongly associated with the patulous shell type, differences in animal characteristics associated with shell type would be apparent and appear to support a division based on shell shape. However, since *L. rudis* can exhibit the '*patula*' form also, a division based on shell shape applied at other sites, e.g. Porth Swtan, where there is no clearcut association of shape and colour with species, would result in a mixture of species in both shell shape categories. This would explain the strong similarity in penis characters recorded here for *L. arcana* and by Heller for *L. patula*, and it also explains the ovoviviparity recorded by Heller for *L. patula* which could have resulted from the admixture of patulous *L. rudis* females.

In spite of the strong association of *L. arcana* with Heller's previously described *L. patula*, it is suggested that the name *L. patula* should henceforth be regarded as a synonym of *L. rudis*. The shell characteristics associated with *L. patula* by Heller and with the patulous shape were those described by Jeffreys (1865). He described var. *patula* in the following terms 'ear-shaped and expanded, thinner, spire not prominent placed somewhat obliquely, mouth wide.' However, as Jeffreys acknowledges, his was not the original description. The original author was C. Thorpe (1844) who described *L. patula* somewhat differently, viz: 'Semi-globose, rather solid, grey-chocolate colour with coarse and rather distant raised spiral striae; whorls three; the aperture occupying three-fourths the length of the shell, peritreme white, throat glossy chocolate.' Thus the original description of *L. patula* does not describe the type of shell with which *L. arcana* is most strongly associated and furthermore *L. arcana* is, on the basis of Thorpe's description, no more closely associated with the *patula* shell type than is *L. rudis*. However at some sites it is possible to separate *L. arcana* and *L. rudis* by the shell, once it has been established which species is associated with which shell characteristic e.g. Abraham's Bosom. If such a difference could be found at the type locality of *L. patula* it would be possible to suggest which species secreted the type shell.

The type locality of *L. patula* is the Eddystone Rock. A small sample was obtained from there, comprised of fourteen specimens of *L. arcana* and three of *L. rudis*. With respect to the original description all the shells were semi-globose, all had three whorls, in all the aperture occupied three-fourths the length of the shell and in all the throat was a glossy chocolate colour; none of the shells had a white peritreme; ridging occurred in ten of the fourteen shells of *L. arcana* (none of the other shells was ridged); none of the shells was a grey-chocolate colour: i.e. none of



the shells fitted exactly the description of the type shell.

Even should a larger sample provide sufficient evidence that the type shell of *L. patula* was secreted by *L. arcana* it would be necessary for a similar proceeding to be undertaken with unequivocal results at all the type localities of all the other shell varieties that *L. arcana* is capable of producing, before any of the shell variety names could be regarded as taking precedence over *L. arcana*.

Since the name *L. patula* appears to be not especially appropriate and *L. arcana* is not particularly associated with any other previously named shell variety, whose name might be used in preference, a new name *L. arcana* has been proposed for this morphologically distinct but conchologically indistinct species.

#### ACKNOWLEDGEMENTS

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APPENDIX A: TYPE MATERIAL

Type locality: Porth Swtan, N. W. Anglesey, Wales. Grid ref: SH 299892.  
Holotype: Female. Shell height=9.35 mm. Collected: 5th March, 1978. Deposited in British Museum (Natural History), London. Registration number: BM 197823 W.  
Paratypes: 21 specimens=10 female (five mature, five immature), 11 male (all mature). Registration number: BM 197824 W.  
Derivatio nominis: “*arcanus*” (Latin) =cryptic, able to keep a secret.

APPENDIX B: OTHER LOCALITIES OF *L. ARCANA*

a) Collector: C. J. Hannaford Ellis  
WALES: Rhos-on-Sea SH 820824  
(Anglesey)  
Porth Trwyn SH 295877 Porth Trefadog SH 289863 Porth Penrhyn-Mawr SH 285839  
Ynys Peibio SH 259824 Ynys Wellt SH 234839 Porth Namarch SH 226835 Abraham’s  
Bosom SH 215813 Trearddur Bay SH 255787 Rhoscolyn SH 271747 Porth Tre Castell  
SH 332705 Llanddwyn Island SH 386628 Trwyn-y-Penrhyn SH 630798 Bell Rock SH  
639813 Porth Llanlleiana SH 381951 Hen Borth SH 318931  
YORKSHIRE Filey Brigg TA 132816  
SCOTLAND Longniddry NT 437768 North Berwick NT 554855 Dunbar Site 1 NT 679795 Site 2  
NT 687786  
b) Other Collectors:  
EIRE Carnsore Point, Wexford Dr. B. Healy  
FRANCE Le Conquet, Finistère Prof. A. J. Cain  
NORWAY Trondheimsfjord Mr. P. van Marion  
WALES The Wick, Skomer, Dyfed Dr. J. Heller Stackpole Quay, Dyfed Dr. J. Heller Castell  
Dinas Head, Fishguard Bay, Dyfed Dr. J. Heller  
NORTHUMBERLAND Berwick-upon-Tweed Dr. S. Smith  
CHANNEL Eddystone Rock Mr. G. R. Forster



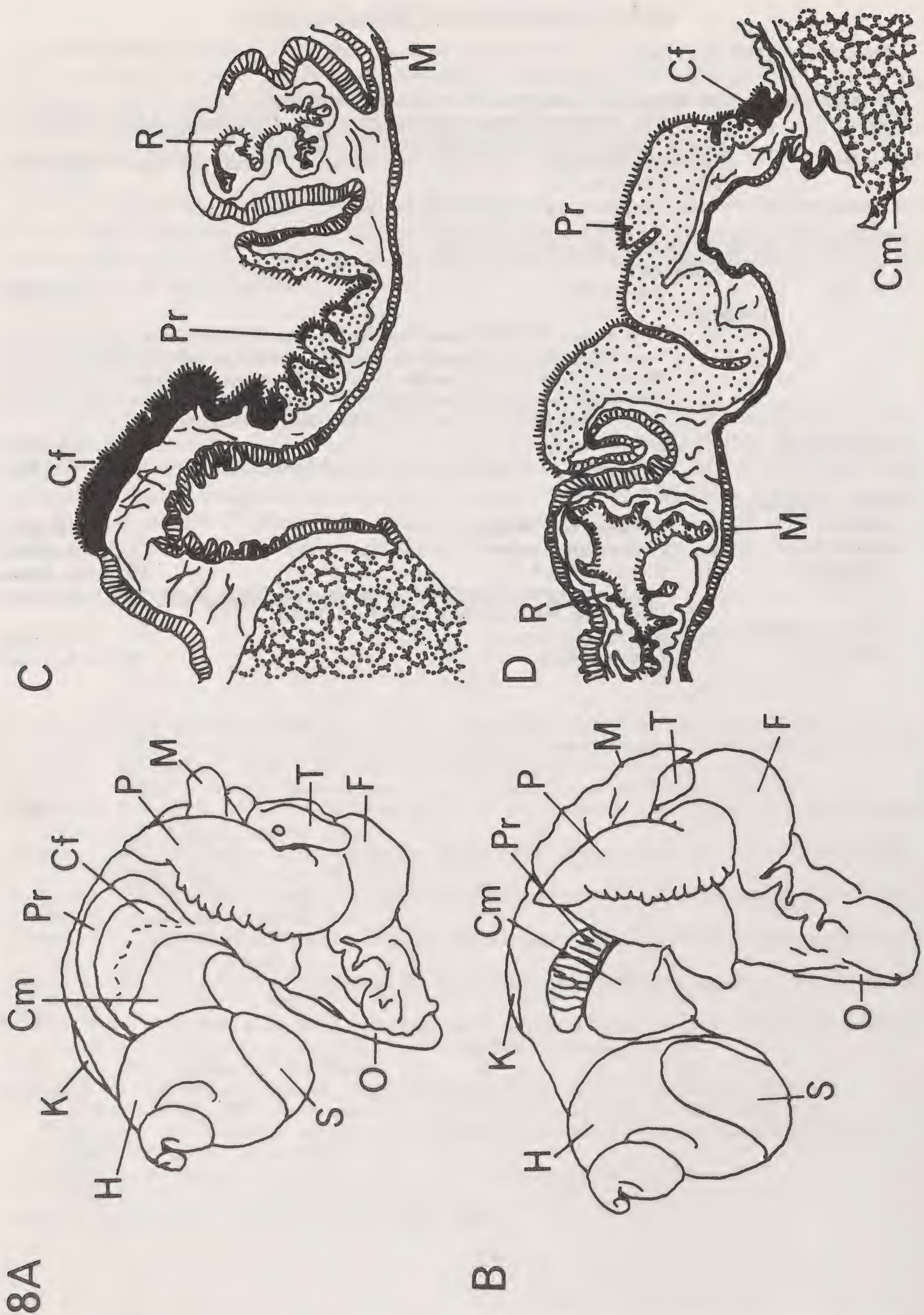


Fig. 8. Diagrams traced from Plate 1. A) *L. rudis* B) *L. arcana* Cf:- ciliated field; Cm:- columellar muscle; F:- foot; H:- hepatopancreas; K:- kidney; M:- mantle; O:- operculum; P:- penis; Pr:- prostate; S:- stomach; T:- tentacle. C) *L. rudis* D) *L. arcana* Cf:- ciliated field; Cm:- columellar muscle; M:- mantle; Pr:- prostate; R:- rectum.



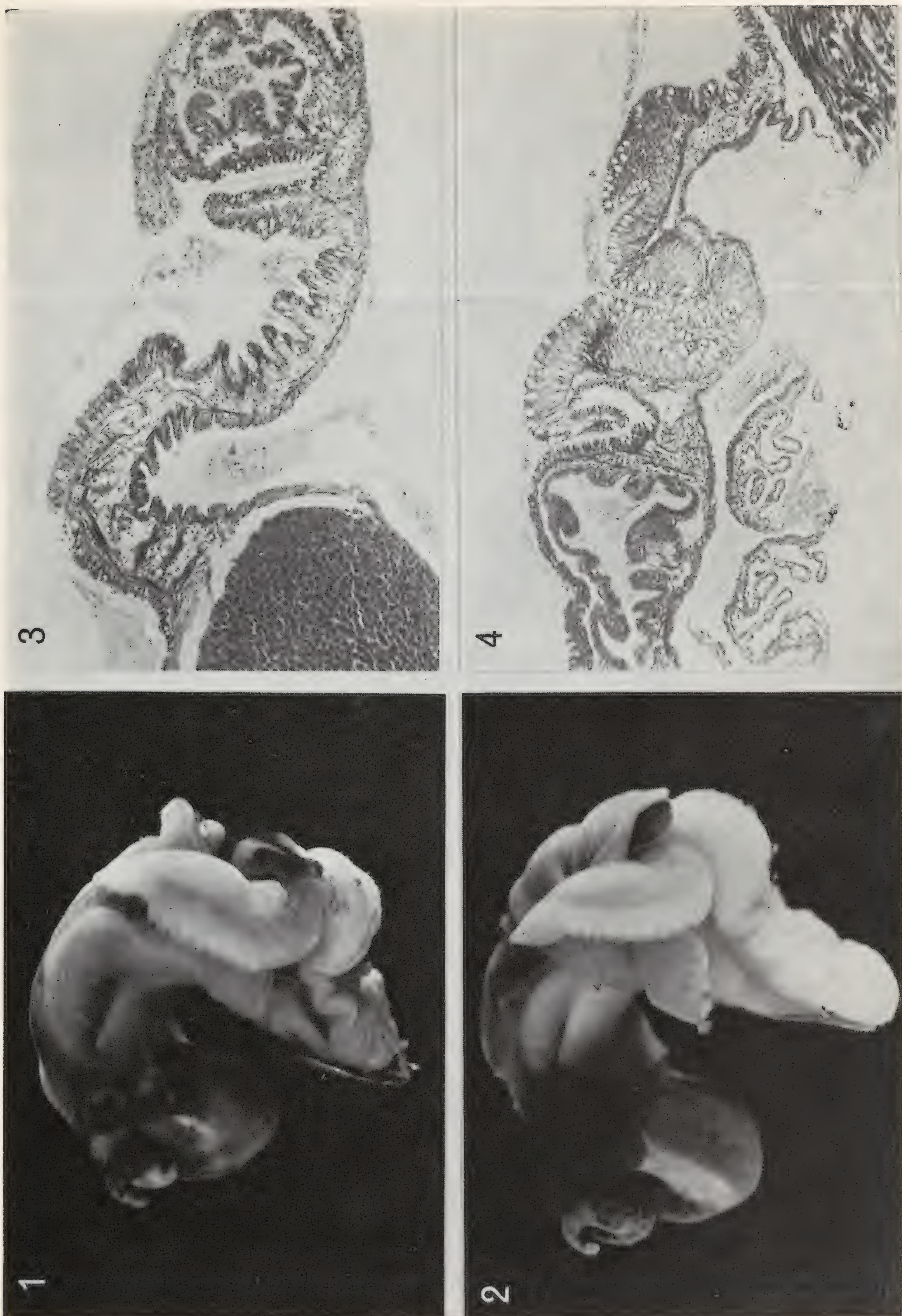


Plate 1. a) mature males removed from shells 1) *L. rudis* 2) *L. arcana* b) T.S. sections through rectum, prostate and ciliated field 3) *L. rudis* 4) *L. arcana*.



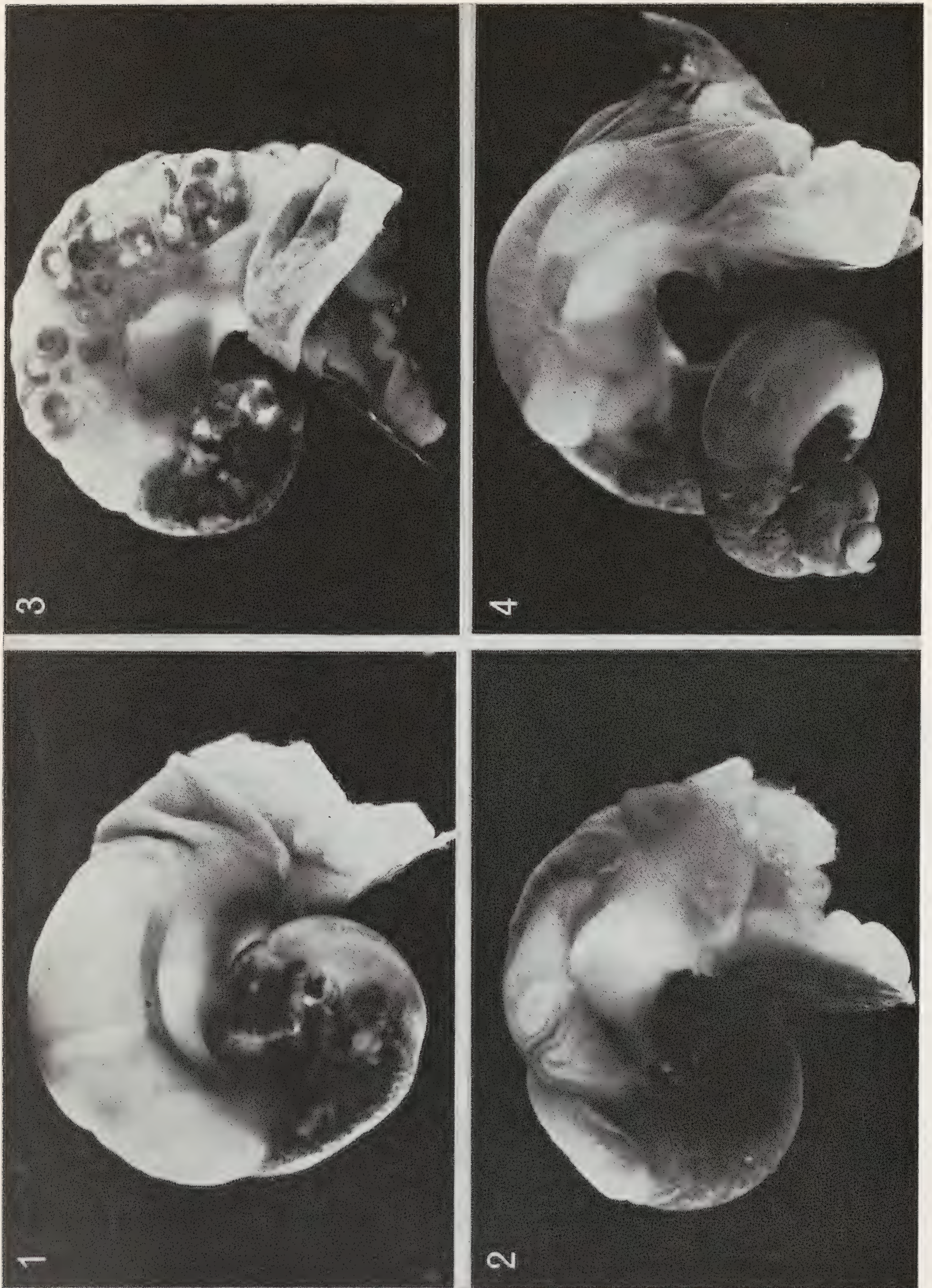


Plate 2. Females removed from shell 1) mature *L. arcana*; 2) immature *L. arcana*; 3) mature *L. rudis*; 4) immature *L. rudis*.



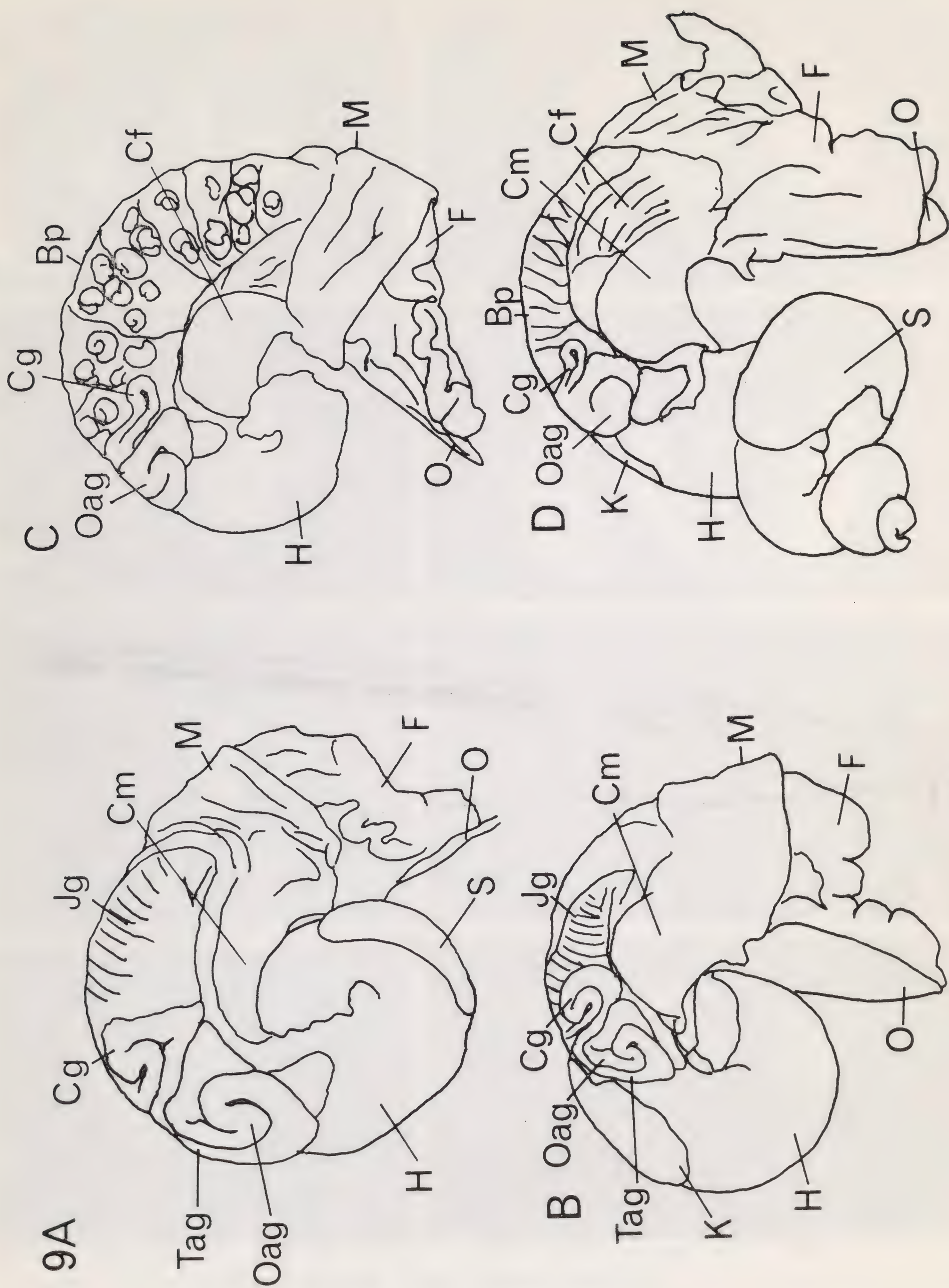


Fig. 9. Diagram traced from Plate 2. A) mature *L. arcana* B) immature *L. arcana* C) mature *L. rudis* D) immature *L. rudis*. Bp: brood pouch; Cf: ciliated field; Cg: capsule gland; Cm: columellar muscle; F: foot; H: hepatopancreas; Jg: jelly gland; M: mantle; O: operculum; Oag: opaque albumen gland; S: stomach; Tag: translucent albumen gland.



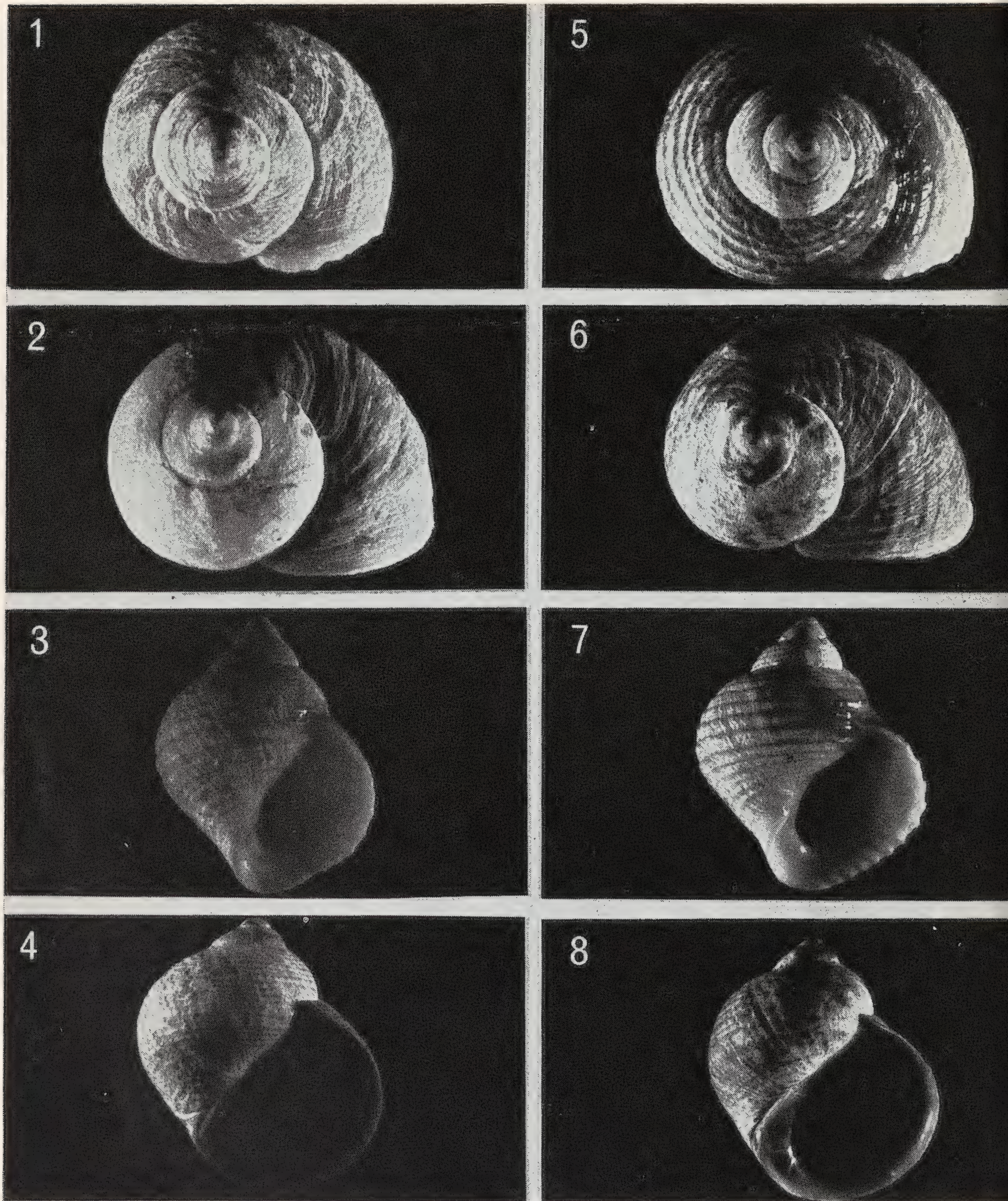


Plate 3. Shells, nos. 1-4, *L. rudis*; nos. 5-8, *L. arcana*.



# THE MARINE MOLLUSCA OF THE UNITED ARAB EMIRATES, ARABIAN GULF

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*Abstract:* This paper presents an annotated list of the Mollusca collected along the coast of the United Arab Emirates within the Arabian (or Persian) Gulf, between As Shaam and Ras Ghanadha, during 1972 and 1973, chiefly by Major M. D. Gallagher, but also by the author. Localities and habitats are given for all Mollusca observed alive and a history of collecting and recording in the Arabian Gulf is included. The molluscan fauna of the northern coast of the United Arab Emirates differs from that of the area around Abu Dhabi and is richer in species. Biggs (1973) listed 97 identified gastropods and 83 identified bivalves from Abu Dhabi. Of these, 23 gastropods and 23 bivalves were not found in the area covered by this paper, while 134 species are common to both areas and another 214 species occur only in the area covered by this paper.

This paper deals with the Mollusca collected between December 1971 and August 1973 along the western shores of the United Arab Emirates, chiefly by Major M. D. Gallagher and by the author during two collecting trips with Major Gallagher in 1972 and 1973. Records were kept of all localities and habitats where live molluscs were found. Other collectors also gave me, or allowed me to record, their finds and their help is much appreciated. The collections of Mollusca covered here were made between Ras Ghanadha in the south and As Shaam, the last accessible point, in the north. They thus complement and add to the records of Biggs (1973) on the Mollusca collected by teams of geologists from Imperial College, University of London, in 1961 and 1965. These latter collections were made in the neighbourhood of Abu Dhabi and the extreme south east of the Qatar Peninsula. Mollusca collected by Major Gallagher and the author along the Gulf of Oman will be dealt with later.

## HISTORY OF COLLECTING AND RECORDING WITHIN THE ARABIAN GULF

For the purposes of this paper the Arabian Gulf (or Persian Gulf, as it is otherwise known) is taken to be the area of water within the Gulf southwards and eastwards from the northern extremities in Kuwait, Iraq and Iran, to an imaginary line drawn between the tip of the Mussandam Pensinsula and the town of Minab on the Iranian mainland.

Many authors (including some present day ones) cause confusion by giving 'Persian Gulf' as a locality, when the area in question is in actual fact in the adjoining Gulf of Oman. The two gulfs are considerably different and there is a resultant difference in the flora and fauna. The Persian Gulf is an area of shallow water and high salinities, into which several major rivers discharge. There is little outflow of water through the Straits of Hormuz as much of the incoming ocean water evaporates. The Gulf of Oman, on the other hand, is deep, with abysses and upwellings of cool water; the tides and salinity of the sea water follow a normal pattern and no major rivers discharge into it. Precise localities and geographical accuracy are needed if molluscan distribution in these regions is to be correctly recorded.



Within this area there was some limited collecting in the nineteenth century in scattered localities. The first recorded list of Mollusca that I have traced is that of Issel (1865), who listed the species deposited in the Italian Mission in Persia collected at Bandar Abbas and Hormuz by G. Doria and R. A. Philippi. Fourteen marine gastropods, one scaphopod and two bivalves were recorded.

E. A. Smith (1877, 1878, 1882 and 1888) described 17 new species of molluscs from material in the British Museum (Natural History) (B.M.N.H.) collected by Col. Sir Lewis Pelly in the Persian Gulf. Material collected by Pelly is also in the Zoology Museum of the University of Cambridge and in the National Museum of Wales, Cardiff. Pelly, who was promoted to Colonel in 1871, was the Political Resident at Bushire from 1862 to 1872. The only recorded locality that I have traced is 'dredged by Col. Pelly in the Persian Gulf at 14 fathoms' (Melvill and Standen, 1901).

E. von Martens (1874) listed the marine Mollusca collected by Dr. Haussknecht at Bushire: a total of 86 gastropods, 2 scaphopods, 30 bivalves and 1 cephalopod. Melvill and Abercrombie's statement (1893) that von Martens enumerated 49 species is incorrect. The Haussknecht list added to those already recorded 64 gastropods, 1 scaphopod, 28 bivalves and 1 cephalopod new to the Gulf. However, I suspect that some of Dr. Haussknecht's shells came from elsewhere as *Cymbium* spp is not recorded for this area by any other author while some of the *Cypraea*, including *C. valentia* Perry and *C. pantherina* Solander are unlikely records and, like Townsend's specimen of *C. mauritiana*, may have been 'bought from a native'.

G. and H. Nevill (1875) added 2 new species collected by W. T. Blanford at Tumb Island within the Arabian Gulf, though most of Blanford's collecting was in the Gulf of Oman. The vast amount of material which he collected was deposited in the Indian Museum and I cannot trace any record of it.

Cooke (1885, 1886) in his papers on the MacAndrew collection from the Gulf of Suez, added distribution records for the Mollusca listed, 'drawn from authentic sources or from private sources of information on which I can rely'. (One of these sources was obviously the Pelly material in the MacAndrew collection). He listed a total of 38 gastropods, 1 scaphopod and 35 bivalves from the Persian Gulf, adding 32 gastropods, 1 scaphopod and 29 bivalves to those already recorded.

Fischer (1891) listed 18 gastropods, 1 scaphopod and 14 bivalves collected by M. F. Houssay at Bushire, adding 7 gastropods and 8 bivalves. Sowerby (1894) in two papers, described 3 new species from shells collected by F. W. Townsend and this was the forerunner of Melvill and Standen's and Melvill's large number of papers dealing with the enormous collections made by Captain Townsend, mostly along the course of the submarine telegraph cable from Karachi to Fao at the head of the Persian Gulf.

Melvill and Standen (1901) and Townsend (1928) give accounts of the method of collecting and of the localities. Most of the material collected is in the B.M.N.H. (including all the type specimens), and in the National Museum of Wales (N.M.W.), where Melvill's own collection is now housed and also that of Miss L. Gunter which was acquired in 1975 (N.M.W. Accession Number 75.23Z). Miss Gunter was obviously a friend of Townsend's, judging from his letters preserved with her collection. She met him through her brother, who lived in Karachi, and she helped to sort the material he obtained. Much of her collection is undetermined material from 156 fathoms, Gulf of Oman. Townsend material is also in various other museums.

Melvill and Standen (1901, 1906) and Melvill (1928) published lists of the Mollusca from the Persian Gulf, Gulf of Oman and North Arabian Sea, purporting to be complete and to include previous records and, in addition to the Townsend material, listing that of the Pelly and Blanford material in the B.M.N.H. However, not only were many of their own records omitted from these lists, they also omitted 9 of Issel's, 44 of von Martens's, 5 of Fischer's and all of Cooke's. For the Persian Gulf, as defined for this paper, they listed a total of 502 gastropods, 2 cephalopods, 7 scaphopods and 148 bivalves, adding 465 gastropods, 2 cephalopods, 6



scaphopods and 129 bivalves to the records already published. They did not record many intertidal species as most of the shells came from the deepest parts of the Gulf on the line of the cable.

Subsequent to 1928 the records for the Persian Gulf were augmented by various workers and their results are tabulated below:

| <i>Author</i>                    | <i>New records.</i>                                                          |
|----------------------------------|------------------------------------------------------------------------------|
| Salisbury (1934)                 | 1 bivalve.                                                                   |
| Thorson (1940)                   | 5 gastropods, 5 opisthobranchs.                                              |
| Haas (1952, 1954)                | 32 gastropods, 24 bivalves.                                                  |
| Eames and Wilkins (1957)         | 4 new species gastropods, 2 new bivalves.                                    |
| Hudson, Eames and Wilkins (1957) | 13 gastropods, 3 bivalves.                                                   |
| Biggs (1958)                     | 15 gastropods.                                                               |
| Biggs and Grantier (1960)        | 4 gastropods, 21 bivalves.                                                   |
| Dance and Eames (1966)           | 5 new species gastropods, 2 new bivalves.                                    |
| Smythe (1972)                    | 14 gastropods, 11 bivalves.                                                  |
| Biggs (1973)                     | 2 chitons, 34 gastropods, 23 bivalves.                                       |
| Vita-Finzi and Cornelius (1973)  | 1 bivalve.                                                                   |
| Tadjalli-Pour (1974)             | 40 gastropods (including 8 undetermined species of Vermetidae), 30 bivalves. |
| Ahmed (1975)                     | 10 gastropods, 5 bivalves.                                                   |

The new species of Hudson, Eames and Wilkins and of Dance and Eames were described from the Recent deposits of Hamar, Iraq; several of these have also been found living within the Gulf.

In enumerating the records above I have omitted all synonyms as emended or quoted by the authors. However, I suspect that many more of the species recorded may well be synonymous with each other. In the taxonomic list I have noted all those of which I know and the actual numbers of species should be a great deal smaller than the sum totals of 854 gastropods, 350 bivalves, and 20 other species, which I have so far traced as having been recorded within the limits which I have defined.

#### THE COASTLINE

The United Arab Emirates, previously known as the Trucial States, border the south eastern coast of the Arabian Gulf and the northwestern coast of the Gulf of Oman. The Mollusca of this latter coastline differ from those of the Arabian Gulf coast and are more akin to those found along the Oman coast. In the south, in the area of Abu Dhabi, the coast is flat and sandy with extensive lagoons, T-shaped islands and fringing reefs. This area is described by Evans (*in* Biggs, 1973). With special reference to the United Arab Emirates coastline within the Gulf, Biggs (1973) lists a total of 100 gastropods, 86 bivalves and 3 opisthobranchs from Abu Dhabi and environs. In May 1973 I visited Abu Dhabi and was able to examine the collections of Mr. and Mrs. P. Dow, members of the Conchological Society of Great Britain and Ireland and those of other experienced collectors. I was also able to collect myself in the company of Mr. and Mrs. Dow and others. I found very few species not recorded by Biggs.

I discussed the differences in molluscan fauna between Abu Dhabi and further north with Dr. M. W. Story, geologist and conchologist, and he suggested that these might be due to the 'Abu Dhabi Divide': the more rapidly emergent coastline of the south characterized by the many T-shaped islands along the coast which may have discouraged the spread of many species. Also the increased salinity of the southern waters may limit the species to those which can tolerate difficult environmental conditions (Evans, Mung, Biggs, Bate and Bush *in* Purser, 1973).



From Jazirat al Bahrani the coast runs northeastwards to culminate in Ru'us al Jabal at the tip of the Mussandam Peninsula. The geology of the northern tip of the peninsula, which is only accessible by sea or by mountain paths over difficult terrain, is covered by Falcon (1973). This paper does not include the Mollusca of this region.

At Jazirat al Bahrani the coastal plain is wide but the coast and mountains converge as one progresses northwards to meet at As Shaam, where the mountains descend steeply into the sea and the beaches end. These mountains, with peaks of up to 2000 m, are of limestone, dolomite and marl, with some metamorphic rocks, chert, and serpentine. At their foot are gravel plains, cut by wadis, merging into the coastal sand dunes of carbonate or quartz and shell fragments, which form a barrier to any surface flow. Subterranean water supplies various date, fruit and vegetable gardens and fresh water seepages occur along the coast in various khawrs (Smythe, 1975).

The coastline in the south is advancing seaward due to deposition of sediment, but further north the long sandy beaches are replaced by steep sand dunes as active dune development is replaced by dune erosion. Long sandy spits protect shallow sheltered creeks with silty or sandy floors. Underlying rocks outcrop in headlands or low cliffs which become more numerous as one goes north. Umm al Qawain is a deep water lagoon of considerable size, protected by sandy and rocky headlands and containing many islets of rock or sand with mangroves, sandbars and coral.

The salinity of the seawater along this coast, measured in March/April 1972 and 1973, was between 42 and 44.5‰. It was slightly higher in the upper reaches of long creeks such as Sharjah, but nowhere approached the very high salinities recorded by Evans (*in* Biggs, 1973) nor those of the true 'sabkha' creeks further north (personal communications, Mrs. L. Johanson and members of the oil company staffs). Even the lower salinities recorded along the United Arab Emirates coast within the Arabian Gulf are higher than that of the Gulf of Oman 38‰ in the same months recorded along the coast between Dibba and Khor Fakkan).

#### COLLECTING LOCALITIES AND HABITATS

For convenience each collecting locality has been allotted a number (Figure 1) and the habitats have been given a lower case letter, thus:

- (a) Rocks, rocky cliffs or structures, breakwaters, oyster colonies serving the purpose of rocks.
- (b) Sandy habitats (beaches, sandy pools and sandy creeks).
- (c) Silty, sludgy or muddy habitats (floors of creeks).
- (d) Deep water habitats (Divers).
- (f) On mangroves or in thick mangrove mud.

- 1 AS SHAAM. The northernmost accessible point. (a) Precipitous rocky headland with isolated rocky outcrops with crevices and sandy bottomed rock pools. (b) Long stretch of sandy beach—coarse sand with pebbles and some rocks at low water.
- 2 GHALILAH (a) Flat rocky headland with boulders.
- 3 KHOR KUWAYR (a) Isolated rocks and rocky creek walls, rocky jetties. (b) Sandy beach facing the Gulf. (c) Creek—silt, mud and some sand. (d) Deep water off shore.
- 4 KHOR QURM (b) Sea beach and sand bars shielding shallow sandy creeks.
- 5 ISLAND WEST OF RAMS (b) Open sandy beach.
- 6 KHOR HULAYLAH (f) Dwarf mangroves and silt on mud; some up rising of fresh water.
- 7 RAS AL KHAIMAH, near AL MATAF (a) Sea wall of rocks.
- 8 KHOR RAS AL KHAIMAH (c) Muddy creek—some sandy patches.
- 9 JAZIRAT AL HAMRA SOUTH TO KHOR AL BAYDAH. (b) Open sandy beach.



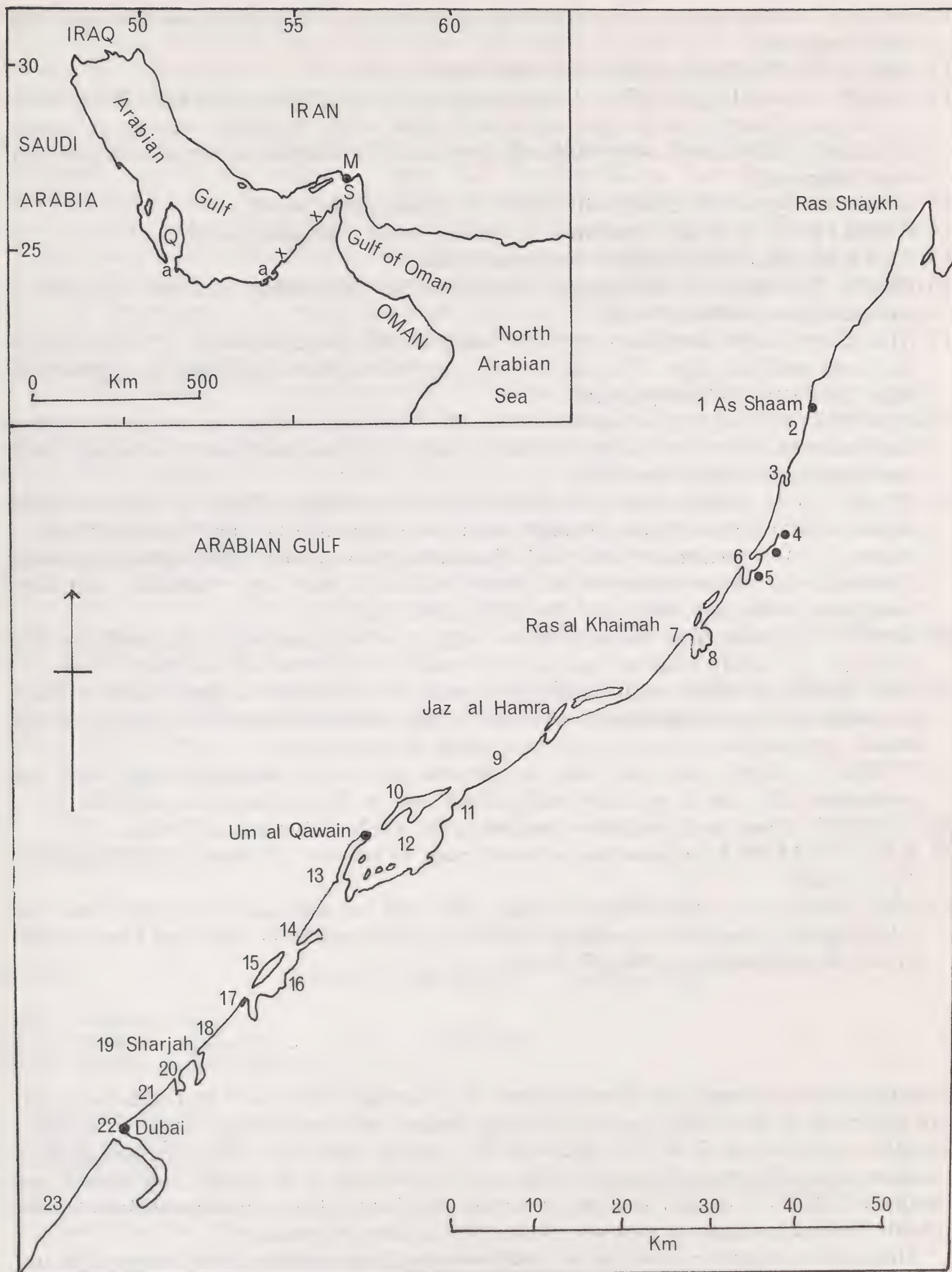


Fig. 1. Collecting localities referred to in the text. Inset map shows the Arabian Gulf. M Minab, Q Qatar Peninsula, S Straits of Hormuz. a-a collecting localities of previous Imperial College expeditions, x-x collecting localities of this paper.



- 10 JAZIRAT SINIYAH (a) Rocky point. (b) Open sandy beach; sandy lagoon with rocks and coral fragments.
- 11 KHOR AL BAYDAH (c) Silt on muddy sand or grit.
- 12 KHOR UMM AL QAWAIN A large lagoon with varying bottom and some living coral.  
(a) Groins of barrels on the sea beach; some loose rocks. (b) Sandy beaches at lagoon entrance. (c) Silt on rock or on lumps of worn coral. (f) Mangroves in mud with rock and coral fragments.
- 13 UMM AL QAWAIN TO HAMRIYAH (b) Open sandy beach.
- 14 HAMRIYAH (b) Sandy headland. (c) Muddy creek with sand patches.
- 15 ZAWRAH ISLAND (b) Open sandy sea beach.
- 16 KHOR ZAWRAH (a) Submerged fragmented flat rocks; rocky outcrops. (c) Creek—intertidal flats of silt and mud.
- 17 AJMAN (a) Rocky outcrops in creek. (b) Sandy headland and sea beach. (c) Creek floor of silt, sand, mud and algae. This was the only area where there was a fairly good growth of algae (probably *Enteromorpha* spp.).
- 18 AJMAN TO SHARJAH (a) Rock outcrops. (b) Open sandy sea beach, backed by a raised beach about a metre above high tide level at one point. This raised beach contained many fossil shells in excellent condition.
- 19 SHARJAH (b) Sandbank and sea beach near creek entrance. There is a shallow sandy lagoon behind the sandbank. Dredged debris was deposited here but contained little of interest. (c) Old town creek—soft mud, silt and sand. Sewage and rubbish here suited some Mollusca, e.g. *Fusinus townsendi*. (f) Inner reaches of the creek. Probably contained mangroves in the past. Intertidal flats of silt and mud.
- 20 KHAN (a) Rocks; large banks of *Ostrea cucullata*, many growing on the sandy or silty substrate. (b) Sandy headland and islet at entrance. (c) Creek: silt and mud.
- 21 ABU HAYL (b) Open sandy beach face (a rocky outcrop here was unproductive). Here accumulates a large quantity of small shells. In this is included those shells collected from a similar area which was not so productive north of Khan creek.
- 22 DUBAI (c) Creek with mud flats, silt, detritus and debris. Sandbanks here were not productive. The area is probably well polluted due to the sizeable port and town.
- 23 JUMEIRA Open sandy extensive beaches to the south of the town of Dubai.
- 24 RAS GHANADHA Not shown on the sketch map. 48 km south of Dubai. (a) Rock shelf. (b) Open beach.
- 25 ABU MUSA One of the offshore islands. This was not accessible during the time this collecting took place, due to political difficulties. For records from this island I am grateful to Mr. Horst Kauch and Mr. M. Nazer.

## RESULTS

*Preliminary notes on taxonomic list.* Identifications of species have been made by comparison with type specimens in the British Museum (Natural History) and the National Museum of Wales, (hereafter referred to as B.M.N.H. and N.M.W.), and by reference to the collections of these museums, especially the collections of Biggs and Winckworth in B.M.N.H. and Melvill and Tomlin in N.M.W. I am also indebted to various world authorities who have helped me with difficult families and species; they are listed in the acknowledgements.

There are many species from this area still awaiting determination. Some may well be unnamed but this author is reluctant to add to the confusion that reigns in this area through the many synonymies that already exist. Many of Melvill and Standen's species are synonymous, not only with other authors' species, but also with their own! The late H. E. J. Biggs (personal communication and manuscript note) commented that he wondered how many examples these



authors had before they described a new species, especially of the smaller genera. Only when one has a large number of these small shells in all conditions from fresh with periostracum, through the various stages of colour loss to completely white, almost featureless ones, can one accurately ascribe them to the correct genus or species.

*Taxonomic list.* The order followed in this list is that of Wenz and Zilch (1938–1961) for the Gastropoda, (with the exception that the Pyramidellacea are listed under the Opisthobranchia), and Moore (1969) for the Bivalvia, as it is convenient to follow standard lists in the main even though there may be points of divergence with more recent opinions.

The named species of Turridae in this list have been checked against the type specimens in the B.M.N.H. Other species have been found, but so far have not been identified with certainty. Where the named species have been discussed by Powell (1966) the generic names have been revised to conform with that work. Species not mentioned by Powell have been given the generic name used by the original author.

Mactridae: Biggs (1973) considered that the *Mactra lilacea/olorina/fauroti* complex needed further study. I have recorded as *M. fauroti* those specimens which have a brown periostracum and which appear to me distinct; as *M. lilacea* the violet-rayed specimens which are violet inside; and as *M. olorina* those which are white throughout. I have an open mind on the two latter species but consider keeping the records separate useful for future studies.

The synonyms listed in column 2 are not intended to be a full synonymy, but a record of other names by which these species have been recorded by various authors within the area of this paper (including known erroneous determinations). These names have been reached by the authors' own corrections, by personal research, by reference to various published synonymies and by use of the unpublished notes of the late H. E. J. Biggs. The authorities quoted therein have not been checked and some may be incorrect.

The localities are given as numbers, corresponding to the numbers in the list of localities. (L) indicates that the molluscs were found alive. The final column indicates the abundance or otherwise of the species:

- A = abundant,
- C = common,
- R = rare,
- U.C.= uncommon.

| SPECIES                                      | SYNONYMS OR ERRORS                                                 | LOCALITIES                            |
|----------------------------------------------|--------------------------------------------------------------------|---------------------------------------|
| CLASS: GASTROPODA                            |                                                                    |                                       |
| SUB-CLASS: PROSOBRANCIA                      |                                                                    |                                       |
| ORDER: ARCHAEOGASTROPODA                     |                                                                    |                                       |
| PLEUROTOMARIACEA.                            |                                                                    |                                       |
| <i>Scissurella jacksoni</i> Melvill, 1904    |                                                                    | 17, 21. R                             |
| <i>Scissurella peilei</i> Winckworth,*       |                                                                    | 24. R                                 |
| <i>Diodora funiculata</i> (Reeve, 1850)      |                                                                    | 16a(L) 1a(L): 3, 9, 17, 19, 20, 21. C |
| <i>Diodora imbricata</i> (Sowerby, 1862)     |                                                                    | 21. R                                 |
| <i>Diodora ruppelli</i> (Sowerby, 1834)      |                                                                    | 12a(L): 3, 8, 9, 17, 24. R            |
| PATELLACEA                                   |                                                                    |                                       |
| <i>Cellana radiata</i> (Born, 1778)          | <i>C. novemradius</i> (Quoy and Gaimard), <i>C. aster</i> (Reeve). | 1a(L) 3(a)L: 21 C                     |
| <i>Cellana karachiensis</i> Winckworth, 1930 |                                                                    | 1a(L) 3(a)L. C                        |



| SPECIES                                                      | SYNONYMS OR ERRORS                                                            | LOCALITIES                                                      |
|--------------------------------------------------------------|-------------------------------------------------------------------------------|-----------------------------------------------------------------|
| TROCHACEA                                                    |                                                                               |                                                                 |
| <i>Turcica stellata</i> A. Adams, 1863                       | <i>T. armatus</i> Issel                                                       | 21 R                                                            |
| <i>Euchelus asper</i> (Gmelin, 1791)                         |                                                                               | 2a(L) 3a(L) 10a(L) 12a(L)<br>16a(L) 20a(L). A                   |
| <i>Euchelus bicinctus</i> (Philippi, 1849)                   |                                                                               | 10, 14, 17, 21. R                                               |
| <i>Euchelus foveolatus</i> (A. Adams, 1851)                  | Var. <i>E. angulatus</i> Melvill                                              | 9, 14, 17, 21, 24. U.C.                                         |
| <i>Solariella biangulosa</i> (A. Adams, 1854)                |                                                                               | 10, 12, 14. R                                                   |
| <i>Solariella solanderi</i> (Philippi, 1849)                 |                                                                               | 3b, 1b. R                                                       |
| <i>G. (Forskaelena) declivis</i> (Forsskäl, 1817)            |                                                                               | 21. R                                                           |
| <i>Trochus erythraeus</i> Brocchi, 1821                      |                                                                               | 1b(L), 3b(L), 1c(L). Cast up<br>all beaches. (dead) C           |
| <i>Trochus radiatus</i> (Gmelin, 1791)                       |                                                                               | 12b. R                                                          |
| <i>Clanculus pharaonis</i> (Linnaeus, 1758)                  |                                                                               | 8. R                                                            |
| <i>Minolia holdsworthiana</i> (G. and H. Nevill, 1871)       |                                                                               | 9, 17, 19b, 21, 24. U.C.                                        |
| <i>Monilea obscura</i> (Wood, 1828)                          |                                                                               | All sandy, and sandy/silty/rocky<br>beaches and creeks. Live. A |
| <i>Umbonium vestiarius</i> (Linnaeus, 1758)                  |                                                                               | Cast up dead all sandy beaches. C                               |
| <i>Stomatia phymotis</i> Helbling, 1779                      |                                                                               | 23. R                                                           |
| <i>Stomatella duplicata</i> Sowerby, 1854                    |                                                                               | 16. R                                                           |
| <i>Teinostoma carbonnieri</i> Jousseau, 1881                 |                                                                               | 17. R                                                           |
| <i>Cyclostrema quadricarinatum</i> Melvill and Standen, 1901 |                                                                               | 10, 14, 19b, 21. C                                              |
| <i>Cyclostrema quinquecarinatum</i> Melvill, 1905            |                                                                               | 21. R                                                           |
| <i>Cyclostrema ocrinium</i> Melvill and Standen, 1901        |                                                                               | 21. R                                                           |
| <i>Cyclostrema placens</i> (Melvill and Standen, 1901)       |                                                                               | 21. R                                                           |
| <i>Homalopoma roseopunctata</i> (Angas, 1880)                |                                                                               | 19c. R                                                          |
| <i>Turbo coronatus</i> Gmelin, 1791                          |                                                                               | All rocky areas live. A                                         |
| <i>Turbo radiatus</i> Gmelin, 1791                           |                                                                               | 1b(L), 17b, 19b. U.C.                                           |
| <i>Tricolia fordiana</i> Pilsbry, 1888                       | <i>T. elachista</i> Melvill, <i>T. minima</i> Melvill,                        | 14. R                                                           |
| <i>Phasianella solida</i> (Born, 1778)                       | <i>P. variegata</i> Lamarck, <i>P. nivosa</i> Reeve, <i>P. jaspidea</i> Reeve | 10, 15, 17, 19, 21. U.C.                                        |
| NERITACEA                                                    |                                                                               |                                                                 |
| <i>Nerita albicilla</i> Linnaeus, 1758                       |                                                                               | 3b(L), 12b(L), 16b(L), 20b(L). C                                |
| <i>Nerita polita</i> Linnaeus, 1758                          |                                                                               | 10b(L), 16b(L). U.C.                                            |
| <i>Nerita adenensis</i> Mienis, 1978                         |                                                                               | 16b(L). U.C.                                                    |
| <i>Smaragdia souverbiana</i> (Montrouzier, 1863)             | <i>S. rangiana</i> Recluz in error.                                           | 16c(L), 17c(L), 14, 19b, 21. U.C.                               |
| <i>Phenacolepas arabicus</i> Ruepell in Thiele, 1909         |                                                                               | 15, 10. U.C.                                                    |
| <i>Phenacolepas evansi</i> Biggs, 1973                       |                                                                               | 17, 19, 21. U.C.                                                |
| ORDER: MESOGASTROPODA                                        |                                                                               |                                                                 |
| LITTORINACEA                                                 |                                                                               |                                                                 |
| <i>Littorina scabra</i> (Linnaeus, 1758)                     |                                                                               | 1a(L), 3(a)(L), 3b(L), 14b. C                                   |



SMYTHE: MARINE MOLLUSCA OF UNITED ARAB EMIRATES

| SPECIES                                                | SYNONYMS OR ERRORS                                                                                         | LOCALITIES                                                |      |
|--------------------------------------------------------|------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------|------|
| <i>Nodilittorina millegrana</i> (Philippi, 1848)       | <i>Littorina granocostata</i> Reeve, <i>L. miliaris</i> Quoy and Gaimard, <i>Tectarius granularis</i> Gray | 3a(L), 6f(L), 16a(L).                                     | U.C. |
| <i>Peasiella isseli</i> (Semper in Issel, 1869)        |                                                                                                            | 10, 16.                                                   | U.C. |
| RISSEOACEA                                             |                                                                                                            |                                                           |      |
| <i>Iravadia annulata</i> (Dunker, 1860)                | <i>I. trochlearis</i> Gould                                                                                | 21.                                                       | R    |
| <i>Cingula (Setia) tiberiana</i> Issel, 1869           |                                                                                                            | All tide lines on sandy beaches<br>Dubai to Um al Qawain. | U.C. |
| <i>Cingula (Hyalia) vitrea</i> (Montagu, 1803)         | <i>Aclis atameles</i> Melvill                                                                              | 21.                                                       | R    |
| <i>Pyramidelloides miranda</i> (A. Adams, 1861)        |                                                                                                            | 14.                                                       | R    |
| <i>Morchiella moreleti</i> (Fischer, 1877)             |                                                                                                            | 17.                                                       | R    |
| <i>Amphithalamus microthyra</i> (von Martens, 1880)    |                                                                                                            | 14, 21, 24.                                               | U.C. |
| <i>Rissoina seguenziana</i> (Issel, 1869)              | <i>R. erythraea</i> Philippi                                                                               | 9, 21.                                                    | U.C. |
| <i>Rissoina clathrata</i> (A. Adams, 1851)             | <i>R. savignyi</i> Jousseaume.                                                                             | 21.                                                       | R    |
| <i>Rissoina distans</i> (d'Anton, 1839)                | <i>R. canaliculata</i> Melvill                                                                             | 17, 21.                                                   | C    |
| <i>Omalogyra atomus</i> (Philippi, 1847)               |                                                                                                            | 21.                                                       | R    |
| <i>Iraquirissoa xanthias</i> (Watson, 1886)            |                                                                                                            | 17, 21.                                                   | R    |
| CERITHIACEA                                            |                                                                                                            |                                                           |      |
| <i>Turritella cochlea</i> Reeve, 1849                  |                                                                                                            | 17c(L).                                                   | U.C. |
| <i>Turritella spectrum</i> Reeve, 1849                 |                                                                                                            | 3, 14, 15, 20, 21.                                        | U.C. |
| <i>Turritella torulosa</i> Kiener, 1843                |                                                                                                            | 1, 3, 9, 12, 17, 19.                                      | C    |
| <i>Torinia buschi</i> Dautzenberg and Fischer,*        |                                                                                                            | 14.                                                       | R    |
| <i>Pseudomalaxis cf zancleus</i> (Philippi, 1844)      |                                                                                                            | 21.                                                       | R    |
| <i>Architectonica perspectiva</i> (Linnaeus, 1767)     |                                                                                                            | 1, 3, 9.                                                  | R    |
| <i>Vermetus sulcatus</i> Lamarck, 1818                 |                                                                                                            | 10a(L), 12a(L), 3, 14, 21, 25.                            | U.C. |
| <i>Caecum cf sepimentum</i> Folin, 1868                |                                                                                                            | 21.                                                       | R    |
| <i>Planaxis sulcatus</i> (Born, 1778)                  |                                                                                                            | 7a(L), 12a(L), 16a(L), 17a(L), 20a(L), 24a(L).            | C    |
| <i>Pirinella conica</i> (Blainville, 1826)             | <i>P. cauillaudi</i> Potiez and Michaud                                                                    | All muddy or silty creeks and mangrove areas.             | C    |
| <i>Cerithidea cingulata</i> (Gmelin, 1791)             |                                                                                                            | All muddy creeks and mangrove areas.                      | A    |
| <i>Terebralia palustris</i> (Brugière, 1792)           |                                                                                                            | 14 (sub fossil). All raised beaches.                      | C    |
| <i>Finella pupoides</i> A. Adams, 1860                 |                                                                                                            | 14, 19, 21.                                               | U.C. |
| <i>Finella purpureoapicata</i> Preston, 1905           | <i>F. cerithina</i> Philippi in error                                                                      | 3b, 9b, 10, 12b, 19b.                                     | C    |
| <i>Finella scabra</i> A. Adams, 1860                   |                                                                                                            | 17.                                                       | R    |
| <i>Scaliola arenosa</i> A. Adams, 1869                 |                                                                                                            | 12b, 14, 22b, 21.                                         | U.C. |
| <i>Scaliola bella</i> A. Adams, 1860                   |                                                                                                            | 21.                                                       | R    |
| <i>Scaliola elata</i> (Semper in Issel, 1869)          |                                                                                                            | 21.                                                       | R    |
| <i>Diala goniocheila</i> (A. Adams, 1840)              |                                                                                                            | 14, 19b, 21.                                              | U.C. |
| <i>Diala semistriata</i> (Philippi, 1849)              | <i>D. macula</i> Recluz                                                                                    | 1b, 12b, 19, 21.                                          | C    |
| <i>Diala sulcifera</i> A. Adams, 1862                  |                                                                                                            | 1b, 3b, 14, 17, 19, 21, 22, 24.                           | C    |
| <i>Diala trilirata</i> Melvill, 1906                   |                                                                                                            | 21.                                                       | R    |
| <i>Alaba virgata</i> (Philippi, 1849)                  |                                                                                                            | 3b, 9, 14, 17, 19, 21, 22, 24.                            | C    |
| <i>Bittium atramentarium</i> Melvill and Standen, 1901 |                                                                                                            | 21.                                                       | R    |



| SPECIES                                                          | SYNONYMS OR ERRORS                | LOCALITIES                                        |      |
|------------------------------------------------------------------|-----------------------------------|---------------------------------------------------|------|
| <i>Bittium tenthrenoïs</i> Melvill, 1896                         |                                   | 10a(L), 21,                                       | R    |
| <i>Clava fasciatum</i> (Bruguère, 1792)                          |                                   | 1, 3, 9, 17, 19.                                  | U.C. |
| <i>Cerithium rugosum</i> (Wood, 1828)                            |                                   | All localities, all habitats.                     | A    |
| <i>Cerithium morus</i> (Lamarck, 1822)                           | ? <i>C. clypeomorus</i> Jousseume | All rocky areas.                                  | C    |
| <i>Cerithium scabridum</i> Philippi, 1848                        | <i>C. yerburyi</i> Smith          | All localities, all habitats.                     | A    |
| <i>Plesiotrochus ?souverbianus</i> Fischer, 1878                 |                                   | 21.                                               | R    |
| <i>Cerithiopsis bandorensis</i> Melvill, 1892                    |                                   | 21.                                               | R    |
| <i>Cerithiopsis hinduorum</i> Melvill, 1898                      |                                   | 10, 14, 19, 21.                                   | U.C. |
| <i>Cerithiopsis semipicta</i> Gould, 1861                        |                                   | 21.                                               | R    |
| <i>Cerithiopsis sykesi</i> Melvill, 1896.                        |                                   | 21.                                               | R    |
| <i>Triphora acuta</i> (Kiener, 1841)                             |                                   | 21.                                               | U.C. |
| <i>Triphora aegle</i> (Jousseume, 1884)                          |                                   | 21.                                               | U.C. |
| <i>Triphora cingulata</i> A. Adams, 1851                         |                                   | 21.                                               | U.C. |
| <i>Triphora corrugata</i> Hinds, 1843                            |                                   | 21.                                               | C    |
| <i>Triphora incolumnis</i> Melvill, 1918                         |                                   | 14, 21.                                           | R    |
| <i>Triphora interpres</i> Melvill, 1918                          |                                   | 21.                                               | R    |
| <i>Triphora perversa</i> Linnaeus, 1767.                         |                                   | 21.                                               | U.C. |
| SCALACEA                                                         |                                   |                                                   |      |
| <i>Scala aculeatus</i> (Sowerby, 1844)                           |                                   | 21.                                               | R    |
| <i>Scala canephora</i> Melvill, 1906                             |                                   | 21.                                               | R    |
| <i>Scala concinna</i> (Sowerby, 1844)                            |                                   | 19b, 21.                                          | R    |
| <i>Scala crassilabrum</i> Sowerby, 1847                          |                                   | 21.                                               | R    |
| <i>Scala deifica</i> Melvill, 1903                               |                                   | 21.                                               | R    |
| <i>Scala cf schepmani</i> Melvill, 1910                          |                                   | 21.                                               | R    |
| <i>Scala simplex</i> Sowerby, 1894                               |                                   | 21.                                               | R    |
| <i>Janthina janthina</i> (Linnaeus, 1758)                        |                                   | 17, 19b.                                          | R    |
| EULIMACEA                                                        |                                   |                                                   |      |
| <i>Niso venosa</i> Sowerby, 1905                                 |                                   | 3b.                                               | R    |
| AMALTHEACEA                                                      |                                   |                                                   |      |
| <i>Vanikoro sulcata</i> d'Orbigny, 1842                          |                                   | 14.                                               | R    |
| <i>Cheila cicatrosa</i> (Reeve, 1858)                            |                                   | 10.                                               | R    |
| CALYPTRAEACEA                                                    |                                   |                                                   |      |
| <i>Calyptraea pellucida</i> Reeve, 1859                          |                                   | 9, 10, 21.                                        | U.C. |
| <i>Calyptraea edgariana</i> Melvill, 1898                        |                                   | 16, 17, 12, 19, 20, 14.                           | C    |
| <i>Crepidula (Siphopatella) walshi</i> Hermansson in Reeve, 1859 |                                   | 9, 21.                                            | U.C. |
| STROMBACEA                                                       |                                   |                                                   |      |
| <i>Xenophora caperata</i> Philippi, 1849                         |                                   | 9.                                                | R    |
| <i>Strombus decorus persicus</i> Swainson, 1821                  |                                   | All sandy localities. (L)                         | A    |
| <i>Strombus fusiformis</i> Sowerby, 1842                         |                                   | 17b(L).                                           | R    |
| NATICACEA                                                        |                                   |                                                   |      |
| <i>Naticina pomatiella</i> Melvill, 1892                         |                                   | 17b, 19b.                                         | U.C. |
| <i>Polinices tumidus</i> (Swainson, 1840)                        | <i>P. mamilla</i> auctt.          | 1, 3, 19b, 16, 20.                                | U.C. |
| <i>Neverita didyma</i> (Roeding, 1798)                           | ? <i>N. bicolor</i> Philippi      | 12b(L), 15b(L), 19b(L). Cast up dead all beaches. | C    |
| <i>Eunaticina papilla</i> (Gmelin, 1791)                         |                                   | 12b(L). Dead all beaches 12 to 19.                | U.C. |
| <i>Natica lineata</i> Lamarck, 1844                              |                                   | 17c(L), 14, 19.                                   | U.C. |



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| SPECIES                                              | SYNONYMS OR ERRORS                                                                                    | LOCALITIES                           |
|------------------------------------------------------|-------------------------------------------------------------------------------------------------------|--------------------------------------|
| CYPRAEACEA                                           |                                                                                                       |                                      |
| <i>Cypraea arabica</i> Linnaeus, 1758                |                                                                                                       | 1a(L), 3a(L), 3d(L). C               |
| <i>Cypraea annulus</i> Linnaeus, 1758                |                                                                                                       | 14. R                                |
| <i>Cypraea carneola</i> Linnaeus, 1758               |                                                                                                       | 14, 20b. R                           |
| <i>Cypraea caurica</i> Linnaeus, 1758                |                                                                                                       | All beaches cast up dead. C          |
| <i>Cypraea fimbriata</i> Gmelin, 1791                |                                                                                                       | 18. R                                |
| <i>Cypraea gracilis</i> Gaskoin, 1848                |                                                                                                       | 1a(L) R                              |
| <i>Cypraea histrio</i> Gmelin, 1791                  |                                                                                                       | 25. R                                |
| <i>Cypraea lentiginosa</i> Gray, 1825                |                                                                                                       | 1a(L), 1b(L), 12b(L). U.C.           |
| <i>Cypraea pulchra</i> Gray, 1824                    |                                                                                                       | 25. R                                |
| <i>Cypraea turdus</i> Lamarck, 1810                  |                                                                                                       | 1a(L), 1b(L), 12b, 14, 19b, 25. C    |
| TONNACEA                                             |                                                                                                       |                                      |
| <i>Semicassis pila</i> (Reeve, 1848)                 |                                                                                                       | 25. R                                |
| <i>Cymatium pileare</i> (Linnaeus, 1758)             |                                                                                                       | 10, 14. R                            |
| <i>Cymatium trilineatum</i> (Reeve, 1844)            | <i>C. tripus</i> Chemnitz                                                                             | 3, 14, 17, 19. U.C.                  |
| <i>Cymatium parthenopeum</i> (von Salis, 1793)       |                                                                                                       | 25(L). R                             |
| <i>Bursa foliata</i> (Broderip, 1844)                |                                                                                                       | 17, 25. R                            |
| <i>Ficus ficoides</i> (Lamarck, 1822)                | <i>F. laevigata</i> Reeve                                                                             | 22, 12. R                            |
| <i>Ficus reticulata</i> (Lamarck, 1822)              |                                                                                                       | Beaches from 1 to 20. U.C.           |
| MURICACEA                                            |                                                                                                       |                                      |
| <i>Rapana bulbosa</i> (Solander in Dillwyn, 1817)    |                                                                                                       | Beaches from 14 to 22. R             |
| <i>Murex kusterianus</i> Tapparone Canefri, 1875     | <i>M. trunculus</i> Linnaeus,<br><i>M. turbinatus</i> Lamarck, <i>M. anguliferus</i> Lamarck          | All sheltered sandy areas live. C    |
| <i>Murex scolopax</i> Dillwyn, 1817                  |                                                                                                       | Cast up dead all beaches, + 25. C    |
| <i>Murex aduncospinosus</i> Sowerby, 1841.           |                                                                                                       | 25. R                                |
| <i>Morula granulata</i> (Duclos, 1832)               |                                                                                                       | 3a. U.C.                             |
| <i>Cronia margariticola</i> (Blainville, 1822)       |                                                                                                       | All rocky areas live. A              |
| <i>Thais mutabilis</i> (Link, 1807)                  | <i>T. carinifera</i> Lamarck                                                                          | All sandy creeks, live. U.C.         |
| <i>Thais savignyi</i> (Deshayes in Lamarck, 1844)    | <i>T. hippocastanum</i> auctt, <i>T. pseudohippocastanum</i> Dautzenberg                              | All rocky areas, live. A             |
| <i>Thais tissoti</i> (Petit, 1853)                   |                                                                                                       | All areas with sand and rock live. C |
| BUCCINACEA                                           |                                                                                                       |                                      |
| <i>Pyrene atrata</i> (Gould, 1860)                   |                                                                                                       | 14, 17, 19, 21. U.C.                 |
| <i>Pyrene phaula</i> (Melvill and Standen, 1901)     | <i>P. selasphora</i> Melvill                                                                          | 21. U.C.                             |
| <i>Mitrella blanda</i> (Sowerby, 1844)               |                                                                                                       | All sheltered creeks live. A         |
| <i>Mitrella cartwrighti</i> (Melvill, 1897)          |                                                                                                       | 14, 17, 19, 21. U.C.                 |
| <i>Mitrella misera</i> (Sowerby, 1844)               | <i>M. zebra</i> Gray                                                                                  | 1a(L), 3a(L), 12a(L), 19a(L). C      |
| <i>Bullia mauritiana</i> (Linnaeus, 1758)            |                                                                                                       | All sandy beaches live. C            |
| <i>Nassarius arcularius plicatus</i> (Roeding, 1798) | <i>N. pullus</i> Linnaeus in error                                                                    | All sandy beaches and creeks live. C |
| <i>Nassarius deshayesiana</i> Issel, 1865            | <i>N. andamanica</i> Melvill and Standen, <i>N. obockensis</i> Jousseume, <i>N. zailensis</i> Sowerby | 21. R                                |
| <i>Nassarius comptus</i> (A. Adams, 1852)            |                                                                                                       | 16. R                                |
| <i>Fusinus townsendi</i> (Melvill, 1899)             | <i>F. arabicus</i> Melvill in error                                                                   | 19c(L), 3b, 9, 10, 12, 22. C         |



| SPECIES                                                         | SYNONYMS OR ERRORS                                                     | LOCALITIES                              |      |
|-----------------------------------------------------------------|------------------------------------------------------------------------|-----------------------------------------|------|
| VOLUTACEA                                                       |                                                                        |                                         |      |
| <i>Ancilla acuminata</i> (Sowerby, 1859)                        |                                                                        | 21.                                     | R    |
| <i>Ancilla castenea</i> (Sowerby, 1830)                         | ? as <i>A. cinnamomea</i> Lamarck                                      | 25(L). Cast up dead all beaches.        | C    |
| <i>Ancilla ovalis</i> (Sowerby, 1859)                           | <i>A. fasciata</i> Reeve in error, <i>A. eburnea</i> Deshayes in error | 12, 17.                                 | U.C. |
| <i>Ancilla scaphella</i> (Sowerby, 1859)                        |                                                                        | 17.                                     | R    |
| <i>Oliva andamanensis</i> Bridgeman, 1909                       |                                                                        | 18.                                     | R    |
| <i>Oliva bulbosa</i> (Roeding, 1798)                            |                                                                        | All sandy areas live.                   | A    |
| <i>Oliva oliva</i> (Linnaeus, 1758)                             | <i>O. ispidula</i> Linnaeus                                            | 3b(L), 1, 9.                            | U.C. |
| <i>Neocancilla clathrus</i> (Gmelin 1791)                       |                                                                        | 15.                                     | R    |
| <i>Gibberula</i> cf. <i>mazagonica</i> (Melvill, 1892)          |                                                                        | 21.                                     | C    |
| <i>Cypraeolina suizensis</i> (Issel, 1869)                      |                                                                        | All sandy tide lines.                   | C    |
| <i>Cypraeolina isseli</i> (G. and H. Nevill, 1875)              | <i>Marginella oodes</i> Melvill                                        | 1, 14.                                  | U.C. |
| CONACEA                                                         |                                                                        |                                         |      |
| <i>Inquisitor griffithi</i> (Gray, 1834)                        | <i>Drillia crenularis</i> Lamarck                                      | 17, 19.                                 | R    |
| <i>Plagiostropha</i> cf. <i>opalus</i> Reeve, 1845              |                                                                        | 21.                                     | R    |
| <i>Eucythara lyrica</i> (Reeve, 1846)                           |                                                                        | 21.                                     | R    |
| <i>Mangelia horneana</i> Smith var. <i>compar</i> Melvill, 1916 |                                                                        | 21.                                     | R    |
| <i>Mangelia</i> cf. <i>posidonia</i> Melvill, 1904              |                                                                        | 21.                                     | R    |
| <i>Mangelia townsendi</i> Sowerby, 1895                         | (Probably <i>M. galigensis</i> Melvill merges)                         | 21.                                     | R    |
| <i>Mangelia recta</i> Smith, 1888                               |                                                                        | 21.                                     | R    |
| <i>Diaugasma epicharta</i> (Melvill and Standen, 1903)          |                                                                        | 21.                                     | R    |
| <i>Conus betulinus</i> Linnaeus, 1758                           |                                                                        | 1b.                                     | R    |
| <i>Conus flavidus</i> Lamarck, 1822                             |                                                                        | 25.                                     | R    |
| <i>Conus omaria</i> Bruguière, 1792                             |                                                                        | 1, 12, 17, 14, 19.                      | U.C. |
| <i>Conus quercinus</i> Solander in Lightfoot, 1786              |                                                                        | 25.                                     | R    |
| <i>Conus striatus</i> Linnaeus, 1758                            |                                                                        | 25.                                     | R    |
| <i>Conus textile</i> Linnaeus, 1758                             |                                                                        | 1, 25.                                  | R    |
| <i>Conus vexillum</i> Gmelin, 1791                              | <i>C. sumatriensis</i> Bruguière                                       | 22.                                     | R    |
| <i>Terebra duplicata</i> (Linnaeus, 1758)                       |                                                                        | 17.                                     | R    |
| <i>Terebra nassoides</i> Hinds, 1843                            |                                                                        | 19.                                     | R    |
| SUB-CLASS:                                                      |                                                                        |                                         |      |
| OPISTHOBRANCHIA                                                 |                                                                        |                                         |      |
| ORDER: ONCHIDIATA                                               |                                                                        |                                         |      |
| ONCHIDIACEA                                                     |                                                                        |                                         |      |
| <i>Onchidium peronii</i> Cuvier, 1805                           |                                                                        | 12a, 12b, 12c, 12f, 16a, 16c (all live) | C    |
| ORDER: TECTIBRANCHIA                                            |                                                                        |                                         |      |
| ACTEONACEA                                                      |                                                                        |                                         |      |
| <i>Solidula affinis</i> A. Adams, 1854                          |                                                                        | 19, 21.                                 | R    |
| <i>Acteon pulchrior</i> Melvill, 1904                           |                                                                        | 21.                                     | U.C. |
| <i>Ringicula propinquans</i> Hinds, 1844                        |                                                                        | 12, 14, 21.                             | U.C. |
| <i>Hydatina velum</i> (Gmelin, 1791)                            |                                                                        | 16.                                     | R    |
| <i>Bullaria ampulla</i> (Linnaeus, 1758)                        |                                                                        | 12b(L), 15(L). All beaches dead.        | C    |
| <i>Atys cylindrica</i> (Helbling, 1779)                         |                                                                        | All tide lines dead.                    | C    |
| <i>Diniatys dentifer</i> (A. Adams, 1850)                       |                                                                        | 25.                                     | R    |



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| SPECIES                                                                     | SYNONYMS OR ERRORS                                                     | LOCALITIES                      |      |
|-----------------------------------------------------------------------------|------------------------------------------------------------------------|---------------------------------|------|
| <i>Haminea vitrea</i> (A. Adams, 1858)                                      |                                                                        | 6c(L), 16, 17.                  | U.C. |
| <i>Retusa truncatula</i> Bruguière, 1792                                    |                                                                        | 19, 21.                         | U.C. |
| <i>Retusa</i> sp. nov.                                                      |                                                                        | 3, 9, 12, 14, 19, 21.           | U.C. |
| <i>Tornatina involuta</i> (G. and H. Nevill, 1871)                          |                                                                        | 21.                             | C    |
| <i>Tornatina persiana</i> Smith, 1872                                       |                                                                        | 17, 21.                         | C    |
| <i>Philene</i> cf. <i>orientalis</i> A. Adams, 1854                         |                                                                        | 12.                             | R    |
| PYRAMIDELLACEA                                                              |                                                                        |                                 |      |
| <i>Odostomia antelia</i> Melvill, 1896                                      |                                                                        | 21.                             | R    |
| <i>Odostomia major</i> Melvill and Standen, 1901                            |                                                                        | 21.                             | R    |
| <i>Chrysallida</i> ( <i>Besla</i> ) <i>edgari</i> (Melvill, 1896)           |                                                                        | 21, 14, 17, 12b, 10.            | R    |
| <i>Chrysallida</i> ( <i>Pyrgulina</i> ) cf. <i>callista</i> (Melvill, 1892) | <i>Pyrgulina mayi</i> Tate, <i>P. bartschi</i> Dautzenberg and Fischer | 21.                             | R    |
| <i>Kleinella</i> ( <i>Acteopyramis</i> ) <i>amaena</i> (A. Adams, 1851)     |                                                                        | 10, 12b, 14, 17, 21.            | U.C. |
| <i>Eulimella gedrosica</i> Melvill, 1904                                    |                                                                        | 21.                             | R    |
| <i>Eulimella kaisensis</i> Melvill, 1898                                    |                                                                        | 21.                             | R    |
| <i>Eulimella squarrosula</i> Melvill, 1918                                  |                                                                        | 21.                             | R    |
| <i>Eulimella venusta</i> Melvill, 1904                                      |                                                                        | 21.                             | R    |
| <i>Turbonilla basilica</i> Melvill, 1897                                    |                                                                        | 21.                             | R    |
| <i>Turbonilla icela</i> Melvill, 1910                                       |                                                                        | 21.                             | R    |
| <i>Turbonilla linjaica</i> Melvill and Standen, 1901                        |                                                                        | 21.                             | R    |
| <i>Turbonilla recticostata</i> Melvill, 1904                                |                                                                        | 21.                             | R    |
| SUB-CLASS: PULMONATA                                                        |                                                                        |                                 |      |
| ORDER: BASOMMATOPHORA                                                       |                                                                        |                                 |      |
| ELLOBIACEA                                                                  |                                                                        |                                 |      |
| <i>Melampus lividus</i> (Deshayes, 1830)                                    |                                                                        | 6                               | U.C. |
| <i>Allochroa bronni</i> Philippi, 1846                                      |                                                                        | 14, 16.                         | R    |
| <i>Plecotrema monilifera</i> H. and A. Adams, 1854                          | <i>Laemodonta rapax</i> Dohrn                                          | 9.                              | R    |
| AMPHIBOLACEA                                                                |                                                                        |                                 |      |
| <i>Salinator fragilis</i> (Lamarck, 1822)                                   |                                                                        | 6f(L), 16c(L), 16c.             | C    |
| SIPHONARIACEA                                                               |                                                                        |                                 |      |
| <i>Siphonaria diemanensis</i> Quoy and Gaimard, 1835                        |                                                                        | 17.                             | R    |
| <i>Siphonaria rosea</i> Hubendick, 1943                                     | <i>S. ashgar</i> Biggs                                                 | 12a(L), 16a(L), 19a(L), 20a(L). | C    |
| CLASS: AMPHINEURA                                                           |                                                                        |                                 |      |
| ORDER: MESOPLACOPHORA                                                       |                                                                        |                                 |      |
| <i>Ischnochiton yerburyi</i> Smith, 1891                                    |                                                                        | 1a(L).                          | U.C. |
| ORDER: TELEOPLACOPHORA                                                      |                                                                        |                                 |      |
| <i>Acanthopleura haddoni</i> Winkworth, 1927                                |                                                                        | 1a(L).                          | U.C. |
| CLASS: SCAPHOPODA                                                           |                                                                        |                                 |      |
| <i>Dentalium octangulatum</i> Donovan, 1803                                 | <i>D. octogonum</i> Donovan in error                                   | All tide lines.                 | A    |



| SPECIES                                                | SYNONYMS OR ERRORS                                                 | LOCALITIES                                      |      |
|--------------------------------------------------------|--------------------------------------------------------------------|-------------------------------------------------|------|
| <i>Dentalium politum</i> (Linnaeus, 1758)              |                                                                    | 9, 17, 21.                                      | U.C. |
| <i>Dentalium tomlini</i> Melvill, 1918.                |                                                                    | 9.                                              | R    |
| CLASS: BIVALVIA                                        |                                                                    |                                                 |      |
| SUB-CLASS: PTERIOMORPHA                                |                                                                    |                                                 |      |
| ORDER: ARCOIDA                                         |                                                                    |                                                 |      |
| ARCACEA                                                |                                                                    |                                                 |      |
| <i>Samacar requiescens</i> (Melvill and Standen, 1906) |                                                                    | 14, 21.                                         | U.C. |
| <i>Anadara antiquata</i> (Linnaeus, 1758)              | <i>A. subrubra</i> Dunker                                          | Cast up on all beaches.                         | C    |
| <i>Anadara ehrenburgi</i> (Dunker, 1868)               |                                                                    | 4, 9.                                           | U.C. |
| <i>Anadara uropygmelana</i> (Bory de St Vincent, 1824) |                                                                    | 3c(L), 12c(L), 17c(L).                          | U.C. |
| <i>Barbatia decussata</i> (Sowerby, 1833)              |                                                                    | 2a(L), 17a(L).                                  | U.C. |
| <i>Barbatia helblingi</i> (Bruguière, 1789)            |                                                                    | 3a(L), 16a(L), 17a(L).                          | C    |
| <i>Barbatia lacerata</i> (Bruguière, 1789)             |                                                                    | Cast up on all beaches.                         | C    |
| <i>Barbatia obliquata</i> (Wood, 1828)                 | <i>B. virescens</i> Reeve, <i>B. divaricata</i> Sowerby            | 1.                                              | R    |
| <i>Acar plicata</i> Dillwyn, 1817                      | <i>A. margarethae</i> Melvill and Standen                          | 12a(L), 10a(L), 16a(L).                         | U.C. |
| <i>Cucullaea labiata</i> Solander, 1786                | <i>C. concamerata</i> Chemnitz                                     | 20.                                             | R    |
| LIMOPSACEA                                             |                                                                    |                                                 |      |
| <i>Glycymeris lividus</i> Reeve, 1844                  | <i>G. heroicus</i> Melvill                                         | 16b(L). Cast up all beaches.                    | C    |
| <i>Glycymeris maskatensis</i> Melvill, 1897            | <i>G. pectunculus</i> (Linnaeus) <i>G. pectiniformis</i> (Lamarck) | 16b(L), 19b(L), 17b(L). All beaches dead.       | C    |
| <i>Glycymeris striatularis</i> (Lamarck, 1819)         | <i>G. spurcus</i> (Reeve)                                          | 9b(L). Cast up all beaches.                     | C    |
| ORDER: MYTILOIDA                                       |                                                                    |                                                 |      |
| MYTILACEA                                              |                                                                    |                                                 |      |
| <i>Brachidontes variabilis</i> (Krauss, 1848)          |                                                                    | All rocky areas and on oyster colonies.         | A    |
| <i>Septifer bilocularis</i> (Linnaeus, 1758)           |                                                                    | 1a(L), 3a(L).                                   |      |
| <i>Crenella compta</i> H. Adams, 1870                  | <i>C. praeceles</i> Melvill                                        | 21.                                             | R    |
| <i>Lithophaga cumingiana</i> (Reeve, 1858)             |                                                                    | 3a(L), 16a(L).                                  | U.C. |
| <i>Lithophaga malaccana</i> (Reeve, 1858)              |                                                                    | 1a(L), 3a(L).                                   | U.C. |
| <i>Modiolus auriculatus</i> Krauss, 1848               |                                                                    | 16, 21.                                         | U.C. |
| <i>Modiolus rhomboideus</i> (Reeve, 1858)              |                                                                    | 1, 16, 19.                                      | R    |
| <i>Modiolus senhaussi</i> (Reeve, 1858)                |                                                                    | 14a(L), 16a(L). Tide lines 12 to 24.            | U.C. |
| <i>Modiolus subsulcata</i> Dunker, 1856                |                                                                    | 19, 17.                                         | R    |
| <i>Botula cinnamomea</i> (Lamarck, 1801)               |                                                                    | 16a(L), 24.                                     | R    |
| PINNACEA                                               |                                                                    |                                                 |      |
| <i>Pinna bicolor</i> (Gmelin, 1791)                    | <i>P. atropurpurea</i> Sowerby, <i>P. mutica</i> Reeve             | 12b(L), 15b(L), 17b(L), 19b(L), 20b(L), 21b(L). | C    |



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| SPECIES                                            | SYNONYMS OR ERRORS                                    | LOCALITIES                                                            |
|----------------------------------------------------|-------------------------------------------------------|-----------------------------------------------------------------------|
| ORDER: PTERIOIDA                                   |                                                       |                                                                       |
| PTERIACEA                                          |                                                       |                                                                       |
| <i>Pinctada margaritifera</i> (Linnaeus, 1758)     |                                                       | 12. R                                                                 |
| <i>Pinctada radiata</i> (Leach, 1814)              |                                                       | 3a(L), 12a(L), 16a(L), 17a(L), 19a(L), 21a(L), on rocks or in weed. C |
| <i>Isognomon legumen</i> (Gmelin, 1791)            |                                                       | 2a(L), 16a(L). R                                                      |
| <i>Isognomon nucleus</i> (Lamarck, 1801)           |                                                       | 6a(L), 17a(L). U.C.                                                   |
| <i>Malleus regula</i> (Førsskål, 1775)             |                                                       | 12a(L). U.C.                                                          |
| <i>Vulsella rugosa</i> Lamarck, 1801               |                                                       | 17, 12 in sponge. R                                                   |
| PECTINACEA                                         |                                                       |                                                                       |
| <i>Chlamys crassicostata</i> Sowerby, 1842         |                                                       | 3b, 14, 19, 22. U.C.                                                  |
| <i>Chlamys plica</i> (Linnaeus, 1758)              |                                                       | 20, 21. R                                                             |
| <i>Chlamys ruschenbergeri</i> (Tryon, 1870)        |                                                       | 12, 17, 19 (free swimming). Cast up dead all beaches. C               |
| <i>Chlamys senatorius</i> (Gmelin, 1791)           |                                                       | 12a(L), 3b, 17, 19, 22. U.C.                                          |
| <i>Plicatula plicata</i> (Linnaeus, 1767)          |                                                       | 2a(L). All rocky areas. C                                             |
| <i>Spondylus hystrix</i> Roeding, 1798             | <i>S. aculeatus</i> Schroeter                         | 14, 16, 21. R                                                         |
| <i>Spondylus gaederopus</i> (Linnaeus, 1758)       | <i>S. exilis</i> Sowerby, <i>S. townsendi</i> Melvill | 3a(L), 12a(L). Raised beach 17, Cast up dead all beaches. C           |
| LIMACEA                                            |                                                       |                                                                       |
| <i>Lima leptocarya</i> Melvill, 1898               |                                                       | 21. R                                                                 |
| OSTREACEA                                          |                                                       |                                                                       |
| <i>Saccostrea cucullata</i> (Born, 1775)           |                                                       | All areas-on rock, mangrove or on each other on sand. A               |
| <i>Ostrea arakensis</i> (Sowerby, 1871)            | <i>O. madrasensis</i> Preston                         | 1, 12, 21. R                                                          |
| <i>Hyotissa hyotis</i> (Linnaeus, 1758)            |                                                       | 12f(L), 21. U.C.                                                      |
| SUB-CLASS: HETERODONTA                             |                                                       |                                                                       |
| ORDER: VENEROIDA                                   |                                                       |                                                                       |
| LUCINACEA                                          |                                                       |                                                                       |
| <i>Divaricella cumingi</i> (Adams and Angus, 1863) | <i>D. dalliana</i> Vanetta in error                   | Cast up on all beaches. C                                             |
| <i>Pillucina fischeriana</i> (Issel, 1869)         |                                                       | Cast up on all beaches. 6c(L). C                                      |
| <i>Anodontia edentula</i> (Linnaeus, 1758)         |                                                       | 19c(L), 6. U.C.                                                       |
| <i>Codakia ?tigerina</i> (Linnaeus, 1758)          |                                                       | 19c. R                                                                |
| <i>Bellucina seminula</i> (Gould, 1861)            | <i>Lucina semperiana</i> Issel                        | 21. R                                                                 |
| <i>Ctena divergens</i> (Philippi, 1850)            |                                                       | 17. R                                                                 |
| <i>Diplodonta ravayensis</i> Sturany, 1901         |                                                       | 17c, 19c, 21. R                                                       |
| CHAMACEA                                           |                                                       |                                                                       |
| <i>Chama pacifica</i> Broderip, 1834               | <i>C. brassica</i> Reeve                              | 3a(L). Cast up on all beaches. C                                      |
| LEPTONACEA                                         |                                                       |                                                                       |
| <i>Scintilla layardi</i> (Deshayes, 1855)          |                                                       | 21. R                                                                 |
| CARDITACEA                                         |                                                       |                                                                       |
| <i>Beguina gubernaculum</i> (Reeve, 1843)          |                                                       | Cast up on all beaches. U.C.                                          |
| <i>Cardita bicolor</i> Lamarck, 1822               | <i>C. antiquata</i> Linnaeus in error                 | 9b(L). Cast up on all beaches dead. C                                 |



| SPECIES                                          | SYNONYMS OR ERRORS                                                                         | LOCALITIES                                     |      |
|--------------------------------------------------|--------------------------------------------------------------------------------------------|------------------------------------------------|------|
| <i>Cardita ffinchi</i> (Melvill, 1898)           |                                                                                            | 10, 17, 19, 21, 25.                            | R    |
| <i>Cuna majeeda</i> Biggs, 1973                  |                                                                                            | 12, 17, 21, 24.                                | U.C. |
| CARDIACEA                                        |                                                                                            |                                                |      |
| <i>Laevicardium papyraceum</i> (Bruguière, 1789) |                                                                                            | 17c(L). All beaches dead.                      | U.C. |
| <i>Parvicardium suzense</i> (Issel, 1869)        |                                                                                            | 14, 21.                                        | R    |
| <i>Trachycardium flavum</i> (Linnaeus, 1758)     |                                                                                            | 17c(L). Cast up on all beaches.                | U.C. |
| <i>Trychycardium lacunosum</i> (Reeve, 1845)     |                                                                                            | 12b(L), 12(L), 16(L), 17c(L) all beaches dead. | C.C. |
| <i>Trachycardium maculosum</i> (Wood, 1815)      |                                                                                            | 12, 20                                         | R    |
| MACTRACEA                                        |                                                                                            |                                                |      |
| <i>Macra fauroti</i> Jousseaume, 1888            |                                                                                            | 15b(L), 17(b)L. Cast up all beaches 1-21.      | C    |
| <i>Macra glabrata lilacea</i> Lamarck, 1818      |                                                                                            | Cast up all beaches.                           | C    |
| <i>Macra olorina</i> Philippi, 1846              |                                                                                            | Cast up all beaches.                           | C    |
| <i>Lutraria angustior</i> Philippi, 1844         |                                                                                            | 19c                                            | R    |
| <i>Meropista nicobarica</i> (Gmelin, 1791)       | <i>Eastonia aegyptica</i> (Gmelin)                                                         | 3, 9, 12, 17, 19, 21.                          | U.C. |
| <i>Ervilia scaliola</i> Issel, 1869              |                                                                                            | 17b(L), 21b(L). All tide lines.                | A    |
| SOLENACEA                                        |                                                                                            |                                                |      |
| <i>Siliqua radiata</i> (Linnaeus, 1758)          |                                                                                            | 3.                                             | R    |
| TELLINACEA                                       |                                                                                            |                                                |      |
| <i>Tellina capsoides</i> (Linnaeus, 1758)        |                                                                                            | 3, 19.                                         | U.C. |
| <i>Tellina claudia</i> Melvill and Standen, 1907 |                                                                                            | 12c(L), 6c(L), 19c(L). All beaches cast up.    | A    |
| <i>Tellina foliacea</i> (Linnaeus, 1758)         |                                                                                            | 3 to 21. Cast up on all beaches:               | U.C. |
| <i>Tellina pharaonis</i> Hanley, 1844            |                                                                                            | 3b.                                            | R    |
| <i>Tellina rastellum</i> Hanley, 1844            | <i>T. dissimilis</i> Deshayes, <i>T. weinkauffi</i> Crosse                                 | 19, 21.                                        | U.C. |
| <i>Tellina wallaceae</i> Salisbury, 1934         |                                                                                            | 9, 19.                                         | U.C. |
| <i>Tellidora pellyana</i> H. Adams, 1873         |                                                                                            | 10, 14, 21.                                    | R    |
| <i>Donax clathratus</i> Deshayes, 1854           | <i>D. pura</i> A. Adams, <i>D. cerasum</i> Sowerby, <i>D. rhomboideus</i> Quoy and Gaimard | 21.                                            | R    |
| <i>Donax scalpellum</i> Gray, 1857               |                                                                                            | 16b(L), 9, 21.                                 | U.C. |
| <i>Gari corrugata</i> (Deshayes, 1854)           |                                                                                            | 9.                                             | R    |
| <i>Gari occidens</i> (Gmelin, 1791)              |                                                                                            | 3, 21.                                         | C    |
| <i>Gari rubicunda</i> (Deshayes, 1854)           |                                                                                            | 19.                                            | R    |
| <i>Gari tripartita</i> (Deshayes, 1854)          |                                                                                            | 3, 9, 1.                                       | U.C. |
| <i>Gari violacea</i> Recluz,*                    |                                                                                            | 16b(L), 3b, 9, 12, 14, 19c, 20.                | C    |
| <i>Asaphis deflorata</i> (Linnaeus, 1758)        |                                                                                            | 3a(L). All beaches 1-22. Cast up.              | C    |
| <i>Iacra seychellarum</i> (A. Adams, 1856)       |                                                                                            | 21.                                            | R    |
| ARCTACEA                                         |                                                                                            |                                                |      |
| <i>Trapezium sublaevigatum</i> (Lamarck, 1819)   |                                                                                            | All rocky sludgy creeks live.                  | C    |
| VENERACEA                                        |                                                                                            |                                                |      |
| <i>Venus reticulata</i> (Linnaeus, 1758)         |                                                                                            | 3.                                             | R    |
| <i>Circe scripta</i> (Linnaeus, 1758)            | <i>C. rivularis</i> Born, <i>C. personata</i> Deshayes                                     | All sandy beaches live.                        | A    |
| <i>Circe abbreviata</i> (Lamarck, 1822)          |                                                                                            | 19.                                            | R    |



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| SPECIES                                          | SYNONYMS OR ERRORS                                      | LOCALITIES                              |      |
|--------------------------------------------------|---------------------------------------------------------|-----------------------------------------|------|
| <i>Circe corrugata</i> (Dillwyn, 1817)           | <i>C. intermedia</i> Reeve                              | 19c(L), 9, 16, 17, 19.                  | C    |
| <i>Circentia callipyga</i> (Born, 1778)          | <i>Circe arabica</i> Lamarck                            | 12c(L), 16c(L), 19c(L).                 | C    |
| <i>Gafrarium pectinatum</i> (Linnaeus, 1758)     | <i>G. divaricatum</i> (Gmelin) <i>G. dispar</i> Dillwyn | 1, 19.                                  | R    |
| <i>Sunetta effossa</i> Hanley, 1842              |                                                         | 9, 21.                                  | R    |
| <i>Sunetta nuda</i> Fischer, 1939                |                                                         | Cast up all beaches.                    | C    |
| <i>Sunetta scripta</i> (Linnaeus, 1758)          |                                                         | Cast up all beaches.                    | C    |
| <i>Meretrix meretrix</i> (Linnaeus, 1758)        | <i>M. zonaria</i> Lamarck                               | All sheltered sludgy creeks live.       | C    |
| <i>Tivela polita</i> (Sowerby, 1851)             |                                                         | Cast up all beaches.                    | U.C. |
| <i>Tivela ponderosa</i> (Koch in Phillipi, 1844) |                                                         | 12c(L). All beaches dead.               | C    |
| <i>Callista albodorsata</i> (Sowerby, 1854)      |                                                         | Cast up all beaches.                    | U.C. |
| <i>Callista lilacina</i> (Lamarck, 1818)         |                                                         | 12.                                     | R    |
| <i>Callista picta</i> (Lamarck, 1818)            |                                                         | 19c.                                    | R    |
| <i>Costacallista erycina</i> (Linnaeus, 1758)    |                                                         | 3b(L). Cast up all beaches.             | C    |
| <i>Dosinia alta</i> (Dunker, 1848)               |                                                         | All beaches 3 to 21.                    | C    |
| <i>Dosinia ceylonica</i> Dunker, 1858            |                                                         | 16c(L). All beaches.                    | U.C. |
| <i>Dosinia exoleta</i> (Linnaeus, 1758)          | <i>D. radiata</i> Reeve                                 | All beaches 3 to 21.                    | U.C. |
| <i>Dosinia hepatica</i> (Lamarck, 1818)          |                                                         | All beaches 3 to 21.                    | U.C. |
| <i>Dosinia histrio</i> (Gmelin, 1791)            | <i>D. globa</i> A. Adams                                | 19c(L), 14.                             | U.C. |
| <i>Dosinia tumida</i> (Gray, 1838)               | <i>D. pubescens</i> Philippi                            | 14, 16, 19.                             | U.C. |
| <i>Tapes textile</i> (Gmelin, 1791)              |                                                         | 25.                                     | R    |
| <i>Irus irus</i> (Linnaeus, 1758)                |                                                         | 12a(L).                                 | U.C. |
| <i>Marcia opima</i> (Gmelin, 1791)               |                                                         | 16c(L), 12(c)L, 19c(L), 20c(L), 17c(L). | C    |
| <i>Paphia gallus</i> (Gmelin, 1791)              |                                                         | 12.                                     | R    |
| <i>Paphia sulcaria</i> (Lamarck 1818)            | <i>P. lentiginosa</i> Reeve                             | Cast up all beaches.                    | C    |
| <i>Venerupis deshayesei</i> Hanley,*             |                                                         | 12, 19.                                 | U.C. |
| <i>Timoclea farsiana</i> Biggs, 1973             |                                                         | 19, 20                                  | U.C. |
| <i>Petricola hemprichi</i> Issel, 1869           |                                                         | 3a(L), 16a(L).                          | U.C. |

ORDER: MYOIDA

MYACEA

|                                         |         |      |
|-----------------------------------------|---------|------|
| <i>Corbula acutangulata</i> Issel, 1869 | 14, 21. | U.C. |
| <i>Corbula sulculosa</i> A. Adams, 1870 | 9.      | R    |

GASTROCHAENACEA

|                                                |        |      |
|------------------------------------------------|--------|------|
| <i>Gastrochaena cuneiformis</i> Spengler, 1783 | 3a(L). | U.C. |
|------------------------------------------------|--------|------|

SUB-CLASS: ANOMODESMATA  
ORDER: PHOLADOMYOIDA

PANDORACEA

|                                           |                       |      |
|-------------------------------------------|-----------------------|------|
| <i>Pandora unguiculus</i> Sowerby, 1830   | 1, 21.                | U.C. |
| <i>Laternula anatina</i> (Linnaeus, 1758) | 3c, 16c, 24c.         | U.C. |
| <i>Laternula</i> sp. nov.                 | 19c(L), 6c, 12c, 20c. | C    |

CLASS: CEPHALOPODA  
SUB-CLASS: DIBRANCHIA  
ORDER: DECAPODA

SEPIACEA

|                                                      |                 |   |
|------------------------------------------------------|-----------------|---|
| <i>Sepiella inermis</i> Férussac and d'Orbigny, 1835 | 12, deep water. | C |
|------------------------------------------------------|-----------------|---|



## SPECIES                      SYNONYMS OR ERRORS                      LOCALITIES

## ARGONAUTACEA

*Argonauta böttgeri* Maltzan, 1881

1, 3.

R

*Argonauta hians* Solander, 1786

1(L).

R

\* Original descriptions not located. Determined by Biggs (*Torinia and Gari*) and by comparison with specimens in N.M.W. (*Scissurella peilei* is probably a manuscript name).

## FIELD AND TAXONOMIC NOTES

## GASTROPODA

*Trochacea*

*Monilea obscura* (Wood). Both this species and *Trochus kotschyi* Philippi have been recorded from the Gulf. Biggs originally separated the two species, but he later showed me a long series in his collection from various localities which ranged from South Africa, along the African coast through East Africa and Somalia to Muscat and throughout the Persian Gulf to Kuwait. He pointed out that this is an extremely variable species and he was convinced that *T. kotschyi* was a synonym. Personal observation in the field has confirmed this view: even within the Arabian Gulf the species is most variable and the differences in the columellar teeth appear possibly to depend on the age of an individual rather than to a locality variation as specimens of the 'kotschyi' form occur in the same community as the more typical 'obscura', as well as intergradations.

Biggs's collection is now in the B.M.N.H.

*Cerithiacea*

*Caecidae*. At least four species of *Caecum* have been found in this area, none of them alive. One has been tentatively identified by comparison with specimens in the Winckworth collection and the rest are being studied by Dr. R. Moore.

*Cypraeacea*

*Cypraea arabica* Linnaeus. Authors either amalgamate *C. arabica* with *C. grayana* Schilder or separate them into two distinct species. Having collected *C. arabica* in the field in East Africa and in the Arabian Gulf and having seen large collections made by others from various localities, I agree with the interpretation that this cowrie is one very variable species. Of the specimens which I have seen, collected from within the Persian Gulf, the 'grayana' humped form seems less common than the form which approaches *C. arabica immanis* Schilder and Schilder.

The appearance of the live animal varies considerably within a single area. The mantle can be reddish, grey or black; the papillae are simple but vary from light to dark. The foot can be pink, tan or grey; the black-tipped siphon varies from red to dark grey. In all the specimens that I have seen the tentacles have always been black.

*Muricacea*

*Murex kusterianus* Tapparone Canefri. Biggs (1973) has discussed the correct name of this species which has been quoted under various names by previous authors. The earliest name, *M. turbinatus* Lamarck, is not available as it is preoccupied by an American species.

*M. kusterianus* has interesting egg-laying habits. Many members of the Muricacea and Buccinacea have a tendency to communal egg-laying, but *M. kusterianus* carries this to an extreme: the individuals commence at a central point, cementing their eggs together in a communal mass. They then proceed to deposit eggs outwards, producing a star-like egg mass. Sometimes late comers join the mass at an intermediate point.



Thorson (1940) discussed the eggs of *M. turbinatus* Lamarck, based on specimens collected from within the Persian Gulf but not collected by himself in person. (Dr. Vera Fretter mentioned to me that Thorson had once expressed to her his great regret that he personally had not always been able to verify the actual specimen which had laid the eggs which he was studying, but had had to rely on the collector's identification.).

Dr. Knudsen kindly lent me the egg masses studied by Thorson, said to be those of *M. turbinatus* Lamarck; these are definitely not the eggs of that species. I have not been able to ascertain exactly which species laid the eggs in question, but it was neither *Thais savignyi* nor *T. tissoti*, the egg masses of which I know. The very small size of the egg capsules would suggest *Cronia margariticola* as a possibility.

*M. kusterianus* varies considerably in proportion, length of fronds and weight of shell. Very old shells become enormously thick and heavy, with very little indication of fronds at all. Some of these variations are illustrated in Biggs (1973).

*Thais savignyi* (Deshayes). Mr. R. N. Kilburn (personal communication) has pointed out to me that *T. pseudohippocastanum* Dautzenberg is a superfluous substitute name for *T. hippocastanum* of authors (non Linnaeus) for which *T. aculeata* (Deshayes) should be used. The species which occurs in the Persian and Oman Gulfs (and elsewhere in the Indian Ocean) is the allied *T. savignyi* (Deshayes). From examination of material in B.M.N.H. and N.M.W. collections, my own collection and that of friends from South Africa and from study of the literature, I am sure that Mr. Kilburn is correct.

#### *Buccinacea*

*Pyrenidae*. *Mitrella blanda* (Sowerby) was noted as almost always being on algae in sandy pools or on sludgy creek bottoms, or burrowing through wet sand just below the surface. *Mitrella misera* (Sowerby) on the other hand was almost always found under algae-covered rocks or stones and was very seldom seen in the open or on sand. The former species survived well in an aquarium in my home, stocked with water and *Enteromorpha* spp. from the nearby Pagham Harbour.

*Nassarius arcularius plicatus* Roeding. Cernohorsky (1972) draws attention to the fact that *N. pullus* (L.) has been recorded erroneously from the Indian Ocean area. I have examined Linnaeus's type of *N. pullus*: it is a strongly humped shell of a peculiar distinctiveness which can not be confused with any other species. My Indian Ocean and Persian Gulf specimens of *N. arcularius plicatus* (and all other members of this family) have been checked by Dr. Cernohorsky and I am confident that all records of *N. pullus* in the Gulf are incorrect.

*N. arcularius plicatus* is very common, crawling in or on wet sand. The animal has a white, semi-translucent foot with a lacy pattern of milky white.

#### *Volutacea*.

*Oliva bulbosa* (Roeding) is common, crawling in wet sand throughout the region. Specimens were observed in Abu Dhabi in April 1973 by Mrs. R. Dow and myself, laying eggs. The mollusc commenced by exuding a mucous mass in which is entrapped several small bivalves (e.g. *Loripes fischeriana* or *Dosinia* spp. juveniles) and enfolded these in the rear portion of the foot. It then crawled along the sand laying a profusion of minute egg capsules in the mucous string attached to the bivalves. Finally it released the bivalves, which burrowed back into the sand taking the egg string with them. One specimen, taken into my hand, complete with the newly attached bivalves, crawled along my hand and arm, laying eggs as it progressed until it had completed laying and released the bivalves.



*Acteonacea.*

*Hydatina velum* (Gmelin). This species was observed alive twice. In May 1972, in late evening on an ebbing tide, Major Gallagher saw them emerging in large numbers from the sand of a creek floor. The following evening he found only a few moribund specimens. Several live collected specimens were despatched to me by airmail. All arrived dead: one pair was in the process of mating and one had been laying eggs. These specimens I put into alcohol and gave them to the late H. E. J. Biggs. They are now in the B.M.N.H. At the same time of day a year later, on a similar low tide, I myself saw this phenomenon—these beautiful animals with their frilly pink mantles, feet and head lobes edged with electric blue were an unforgettable sight as they ploughed up through the sand and crawled through the shallow water in the sunset. Once again, on the following day and on other occasions there was no sign of them.

*Retusidae and Tornatinidae*

These families proved to need a great deal of research and are dealt with in a separate paper.

*Onchidiata*

*Onchidium peronii* Cuvier. This mollusc appears to be equally at home in a wide variety of habitats. It was found on or under rocks in sheltered areas and in the open sea, on sand or mud in creeks and in the mangrove swamps. It displayed no objection to being handled and crawled actively along the hand or arm at times; otherwise it settled on one spot and showed no desire to leave.

## BIVALVIA

*Arcacea.*

Stevenson (1975) puts *Barbatia decussata* (Sowerby) into the synonymy of *B. helblingi* (Bruguère). However, observations in the field suggest the possibility that they may be separate species. *B. helblingi* is found in deep crevices in hard rock, generally difficult to reach and usually mis-shapen because of the restricted habitat. The foot and mantle are white. *B. decussata*, which is more regular in shape, is found in more open and shallower niches, anchored under rocks and even, according to Prashad (1932), often attached to other molluscs. The mantle and foot are deep pink. Further study is needed to decide if these variations are due to environmental differences only.

*Glycymeris maskatensis* Melvill. Kilburn (1975) discusses the differences between *G. maskatensis* and *G. pectunculus* (L.) and points out that the former is the correct name for the species which occurs in the Gulf and the northern part of the Indian Ocean.

*Glycymeris hoylei* Melvill. Biggs (1973) recorded this species for the region in the neighbourhood of Abu Dhabi. I have not seen any specimens of this from the Gulf, nor have I traced any other record, and I have not been able to find the specimen to which Biggs ascribed his record in the B.M.N.H. It is possible that it was an import in ballast.

*Pinnacea*

*Pinna bicolor* Gmelin. Both Rosewater (1961) and Fischer-Piette (1974) assign *P. atropurpurea* Sowerby and *P. mutica* Reeve to the synonymy of the variable *P. bicolor*. Therefore all records of these two species in the Gulf should be read as *P. bicolor*.



*Pectinacea*

*Spondylus gaederopus* (Linnaeus). There has been some hesitation among authors about the correct assignment of the species *S. exilis* Sowerby and *S. gloriandus* Melvill. However, there seems nothing to differentiate these variable species from that of Linnaeus, which is equally variable. A long range of the Gulf specimens shows intergradation between forms with long fine spines and short broad ones, the more common being similar to the more common form of the Mediterranean species. Specimens also occur with the upper and lower valves of different colours: one purple and the other orange or white, for example.

A raised beach at Ajman contains a deep layer of sub-fossil specimens in perfect condition, still showing the original bright colours. The condition of these shells, with their undamaged spines, suggests that they were living in a calm sea and were suddenly overwhelmed by some protective layer before the beach became elevated. The present level of the beach is about 1½ m above high tide level.

At Um al Qawain, a colony of *S. gaederopus* on a groin was seen to have crabs living in the mantle cavities, apparently commensally. Dr. R. W. Ingle, of the British Museum (Natural History), identified the crab as *Ostracoteres spondyli* Nobili. It would appear that the association is well known.

This opportunity is taken to correct an error in Smythe (1972). *S. townsendi* should have read *S. exilis*.

*Leptonacea*

*Scintilla layardi* (Deshayes). Though not found alive in the area of this paper, I have found this species in many areas of the Arabian Gulf. It lives under rocks and in crevices in communities of varying ages in a mass of jelly. The jelly mass adheres to the substrate and the individuals appear to be living loosely within it, not cemented to each other in any way.

*Carditacea*

*Cardita bicolor* Lamarck. This species has been recorded from the Gulf as *C. antiquata* Linnaeus (and as *C. antiquata* Lamarck in error) by several authors. Hanley (1855) states that *C. bicolor* was in the same drawer as Linnaeus's specimen of *C. antiquata* and had been declared erroneously to be the *C. antiquata* of Linnaeus. Presumably he was referring to Reeve's illustration of *C. bicolor* under the name of *C. antiquata* (1843, Pl. 6, fig. 29b). The type of *C. bicolor* in the Musée Nationale d'Histoire Naturelle, Paris, was examined by Dr. M. Tadjalli Pour, who found his specimens from the Gulf to be identical with it. He subsequently checked my specimens against his.

A comparison of Linnaeus's type of *C. antiquata* with my *C. bicolor* from the Gulf showed the two species to be distinct. *C. antiquata* is more rounded in shape; the ribs are rounded in section, not square as in *C. bicolor*; the gaps between the ribs are narrower and *C. antiquata* is finely transversely striate as the author states in his description.

*Cardiacea*

*Trachycardium flavum* (Linnaeus). There are doubts as to the validity of this name. However, the shells for which I am using this name from the Gulf are those figured under this name by Spry (1964). It is distinguishable from *T. lacunosum* most easily by the rounder shape: there are several other differences of a less conspicuous nature.



*Tellinacea*

*Gari tripartita* (Deshayes, 1854). Prashad (1932) puts this species into the synonymy of *G. amethystus* (Wood, 1815). However the descriptions of both authors indicate the differences of sculpture and Wood's figure clearly shows the sinuosity of the central portion of the ridges of *G. amethystus* and the similarity of the ridges on the anterior and posterior parts of the shell. Deshayes (1854) emphasized the lamellose character of the posterior ridges of *G. tripartita* and the type in the B.M.N.H. shows this feature. The sculpture of the anterior third of the shell is of flattened ridges and the central ridges run parallel to the edge of the shell.

*G. tripartita* can be of various shades from pale, pink-rayed specimens to deep violet. All the specimens I have seen have fine pink to violet hairline dashes radiating from the umbo.

*Veneracea*

*Circe scripta* (Linnaeus). Fischer-Piette and Vukadinovic (1975) state that this is a species with many synonyms. Among these are *C. personata* and *C. rivularis* which have been recorded from the Arabian Gulf. It is common in the sandy beaches along the open coastline, burrowing only shallowly and frequently being washed out of the sand by the retreating waves. Surprisingly the molluscs make no attempt to re-bury themselves, but merely lie with their valves closed on the surface of the sand until the tide returns or a predator takes them.

*C. (Circentia) callipyga* (Born). Fischer-Piette and Vukadinovic (1975) give a full synonymy of this species. At least four of these synonyms have been recorded for the Gulf. They put the species into the genus *Gafrarium*, but I am retaining the genus used in the Treatise (Moore, 1969). The species they consider synonymous are certainly very variable. In the present state of knowledge I feel that this synonymy must be accepted.

In the field I have found three distinct forms: the smooth form, *C. callipyga*, which lives in sand in colonies at about the mid inter-tidal level; the coarser, rougher form that I call the 'arabica' form, which lives in shingle or gravel at the low-water mark; and the 'adenensis' form, which seems to be consistently more elongate in shape, always dark coloured inside and which presumably lives in deeper water as we have only found them cast up in a moribund condition after storms (and only from the Gulf of Oman—I have no records from within this area).

*C. (Parmulophora) corrugata* (Dillwyn). Fischer-Piette and Vukadinovic (1975) regard *C. intermedia* as a synonym.

*Gafrarium pectinatum* (Linnaeus). The above authors regard *G. divaricata* as a synonym.

## CEPHALOPODA

*Sepiella inermis* (Férussac and d'Orbigny) was collected by netting by the fishermen at Um al Qawain. They removed the pen and chopped up the animal to use as bait. According to them it was common in that area but they never used any part of the mollusc for food.

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I must express my gratitude to many people. Firstly to Major M. D. Gallagher without whose meticulous collecting and observations and assistance in my field trips, this paper could not have been written. Also to Colonel and Mrs. Carson and Mr. and Mrs. J. Taegar, my hosts,



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There are many others who have helped in many ways and I regret that space does not permit of their names being included: my gratitude to them too, is very deep. Finally I must mention the late Rev. H. E. J. Biggs, my friend and mentor. He identified many of the species listed in this paper, his advice and encouragement was of the greatest help to me and I should like to dedicate this paper to his memory.

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# ON THE OFFSHORE MOLLUSCA OF THE CELTIC SEA

J. P. HARTLEY

Field Studies Council, Oil Pollution Research Unit, Orierton Field Centre, Pembroke, Dyfed, Wales

(Read before the Society, 16 December 1978)

*Abstract:* Details are given of the distribution of 143 species of marine molluscs found during a qualitative benthic survey of the central and northern Celtic Sea. Several records are of zoogeographical interest, generally of northern species at the southern limits of their distributions. A number of rare species was found and the genus *Eleutheromenia* (Mollusca, Solenogastres, Pararrhopaliidae) is added to the British fauna.

The marine molluscs of intertidal and coastal regions of south-west Britain have recently received much attention. There exist marine fauna lists for the Plymouth area (Marine Biological Association, 1957), Dale Fort, Pembrokeshire (Crothers, 1966), and around the Isle of Man (Bruce, Colman and Jones, 1963), as well as an intertidal list for the Severn estuary (Boyden, Crothers, Little and Mettam, 1977). An opisthobranch mollusc list from around Lundy has been compiled by Brown and Hunnam (1976). Withers (1977) describes the soft shore macrobenthos along the south-west coast of Wales. Information on the distribution and abundance of molluscs in coastal waters can be found in Warwick and Davies (1977) for the Bristol Channel and Hunnam and Brown (1975) describe the sublittoral nudibranchs of Pembrokeshire. The English Channel has been studied comparatively intensively, and Holme (1966) gives a list of molluscs found during several surveys. Cabioch (1968) provides information on the molluscs of the western English Channel.

The offshore benthos of the Celtic Sea appears to have been little studied, and it was in view of the paucity of available information and the increased oil industry interest in the area that a survey was undertaken. The survey was designed to investigate qualitatively the distribution of benthic animals and communities over a wide area in the Celtic Sea. A total of 86 stations was sampled, chosen in relation to the blocks licensed for oil exploration in May 1972. A preliminary report of this work has been submitted to the European Economic Community (Hartley and Dicks, 1977), and further results from the survey will be presented elsewhere.

## METHODS

Between September 1974 and August 1975, samples of the seabed fauna and sediments were taken from the following research vessels: R. V. 'Challenger', 42 sites; R. V. 'Prince Madog', 23 sites; R. V. 'Corella', 17 sites; and R. V. 'Kay BB', 4 sites. Information concerning the position of stations, the water depth, the sampling gear used and a visual assessment of sediment type is given in Table 1. Figure 1 shows the locations of the stations and the extent of the survey area.





Fig. 1. Map of the Celtic Sea showing the location and enumeration of the sample sites. The St. Georges Channel lies between the Irish and Celtic Seas.

The benthic epifauna was sampled with a 1 m double-sided Agassiz beam trawl towed for approximately 10 mins. at 1 knot, whilst samples of infauna were taken by grab or dredge.

Preliminary sorting of trawl catches occurred on deck and where a large number of a particular species was present, representative specimens were kept and a recorded number were returned to the sea. Grab and dredge samples were sieved on board through a 1 mm nylon mesh and the retained material was preserved in 4% formalin buffered with hexamine and returned to the laboratory.

A visual assessment of sediment type was made from samples taken from grabs and dredges and, occasionally, sediment-choked trawls.

TABLE 1

Sample Site Information

| Station No. | Position    |             | Depth (m) | Gear Used     | Sediment Type                |
|-------------|-------------|-------------|-----------|---------------|------------------------------|
| 1           | 52° 15.4' N | 05° 18.0' W | 81        | Agassiz trawl | Coarse sand, stones, shells  |
|             |             |             | 81        | Day grab      |                              |
| 2           | 52° 15.6' N | 05° 06.0' W | 52        | Agassiz trawl | Sand, gravel, stones, shells |
|             |             |             | 52        | Day grab      |                              |
| 3           | 52° 03.2' N | 06° 55.5' W | c40       | Agassiz trawl | No data                      |
| 4           | 52° 04.0' N | 06° 06.0' W | 84        | Agassiz trawl | Mud, sand, gravel, stones    |
|             |             |             |           | Pipe dredge   |                              |
|             |             |             |           | Shipek grab   |                              |



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| Station No. | Position    |             | Depth (m) | Gear Used         | Sediment Type                            |
|-------------|-------------|-------------|-----------|-------------------|------------------------------------------|
| 5           | 52° 05.6' N | 05° 42.0' W | 97        | Agassiz trawl     | Sand, gravel, shells                     |
|             |             |             | 97        | Pipe dredge       |                                          |
| 6           | 52° 05.6' N | 05° 30.0' W | 113       | Agassiz trawl     | Mud, coarse sand, gravel, stones, shells |
|             |             |             | 113       | Pipe dredge       |                                          |
| 7           | 51° 55.3' N | 06° 42.0' W | c60       | Agassiz trawl     | Muddy sand                               |
|             |             |             |           | Pipe dredge × 2   |                                          |
| 8           | 51° 55.5' N | 06° 18.0' W | 66        | Agassiz trawl × 2 | Sand, shells                             |
|             |             |             |           | Pipe dredge       |                                          |
| 9           | 51° 55.2' N | 06° 05.0' W | 99        | Agassiz trawl     | Sand, gravel, shells                     |
|             |             |             | 99        | Pipe dredge       |                                          |
| 10          | 51° 55.2' N | 05° 54.1' W | 108       | Agassiz trawl     | Sand, small stones, shells               |
|             |             |             | 108       | Pipe dredge       |                                          |
| 11          | 51° 55.2' N | 05° 42.0' W | 112       | Agassiz trawl     | No data                                  |
| 12          | 51° 55.2' N | 05° 30.0' W | 90        | Agassiz trawl     | No data                                  |
| 13          | 51° 44.8' N | 06° 18.0' W | 81        | Agassiz trawl     | Coarse sand, shells                      |
|             |             |             | 81        | Pipe dredge       |                                          |
| 14          | 51° 45.0' N | 06° 05.0' W | 128       | Agassiz trawl     | Sand                                     |
| 15          | 51° 44.8' N | 05° 54.1' W | 124       | Agassiz trawl     | Stones, shells and ?                     |
| 16          | 51° 38.8' N | 07° 22.0' W | 82        | Agassiz trawl     | Fine, clean gravel                       |
| 17          | 51° 35.0' N | 06° 50.5' W | 73        | Agassiz trawl     | Sandy gravel, shells                     |
| 18          | 51° 35.1' N | 06° 18.0' W | 95        | Agassiz trawl     | Muddy sand, shells                       |
|             |             |             | 95        | Pipe dredge       |                                          |
| 19          | 51° 35.1' N | 06° 05.0' W | 121       | Agassiz trawl     | Muddy sand, shells                       |
|             |             |             | 121       | Pipe dredge       |                                          |
| 20          | 51° 35.1' N | 05° 54.1' W | 122       | Agassiz trawl     | Muddy sand, shells                       |
|             |             |             | 122       | Pipe dredge       |                                          |
| 21          | 51° 24.1' N | 08° 13.0' W | 91        | Agassiz trawl     | Sandy mud, gravel, stones                |
| 22          | 51° 26.8' N | 08° 02.0' W | 86        | Agassiz trawl     | Mud, gravel, large stones                |
| 23          | 51° 25.0' N | 07° 06.5' W | 86        | Agassiz trawl     | Muddy sand, gravel                       |
| 24          | 51° 27.8' N | 06° 34.6' W | 82        | Agassiz trawl     | Muddy sand, shells                       |
| 25          | 51° 24.6' N | 06° 30.0' W | 90        | Agassiz trawl     | Muddy sand, shells                       |
|             |             |             | 90        | Pipe dredge       |                                          |
| 26          | 51° 24.6' N | 06° 18.0' W | 122       | Agassiz trawl     | Mud                                      |
|             |             |             | 122       | Pipe dredge       |                                          |
| 27          | 51° 24.6' N | 06° 05.0' W | 122       | Agassiz trawl     | Mud                                      |
|             |             |             | 122       | Pipe dredge       |                                          |
| 28          | 51° 24.6' N | 05° 54.1' W | 94        | Agassiz trawl     | Muddy sand                               |
|             |             |             | 94        | Pipe dredge       |                                          |
| 29          | 51° 14.9' N | 08° 42.0' W | 104       | Agassiz trawl     | Muddy sand, stones, shells               |
| 30          | 51° 51.1' N | 08° 30.0' W | 104       | Agassiz trawl     | Sandy                                    |
| 31          | 51° 15.0' N | 08° 17.0' W | 99        | Agassiz trawl     | Muddy sand, fine shells                  |
|             |             |             | 99        | Day grab          |                                          |
| 32          | 51° 14.9' N | 08° 06.2' W | 95        | Agassiz trawl     | No data                                  |
| 33          | 51° 17.5' N | 07° 48.4' W | 91        | Agassiz trawl     | Muddy gravel, large stones               |
| 34          | 51° 11.4' N | 07° 32.9' W | 91        | Agassiz trawl     | Sandy gravel, stones, shells             |
| 35          | 51° 15.0' N | 07° 18.1' W | 91        | Agassiz trawl     | Mud, gravel                              |
| 36          | 51° 14.6' N | 06° 41.1' W | 97        | Agassiz trawl     | Sand, gravel, shells                     |
|             |             |             | 97        | Pipe dredge       |                                          |
| 37          | 51° 15.6' N | 06° 30.0' W | 131       | Agassiz trawl     | Mud                                      |
|             |             |             | 128       | Pipe dredge       |                                          |
| 38          | 51° 14.6' N | 06° 18.0' W | 122       | Agassiz trawl     | Mud                                      |
|             |             |             | 122       | Pipe dredge       |                                          |
| 39          | 51° 13.8' N | 06° 05.6' W | 97        | Agassiz trawl     | Mud                                      |
| 40          | 51° 14.6' N | 06° 05.0' W | 108       | Agassiz trawl     | Mud                                      |
|             |             |             | 108       | Pipe dredge       |                                          |
| 41          | 51° 14.6' N | 05° 54.1' W | 95        | Agassiz trawl     | Mud                                      |
|             |             |             | 95        | Pipe dredge       |                                          |
| 42          | 51° 05.9' N | 09° 26.0' W | 119       | Agassiz trawl     | Muddy sand                               |
| 43          | 51° 09.5' N | 09° 07.6' W | 108       | Agassiz trawl     | Clean gravel, stones, shells             |



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| Station No. | Position    |             | Depth (m) | Gear Used               | Sediment Type                    |
|-------------|-------------|-------------|-----------|-------------------------|----------------------------------|
| 44          | 51° 03.9' N | 08° 54.3' W | 110       | Agassiz trawl           | Muddy sand, stones, shells       |
| 45          | 51° 06.5' N | 08° 30.0' W | 104       | Agassiz trawl           | Muddy sand                       |
| 46          | 51° 04.1' N | 08° 16.5' W | 106       | Agassiz trawl           | Soft mud, stones                 |
| 47          | 51° 05.5' N | 08° 08.3' W | 97        | Agassiz trawl           | No data                          |
| 48          | 51° 04.4' N | 07° 18.2' W | 95        | Agassiz trawl           | Muddy sand, shells               |
| 49          | 51° 05.1' N | 06° 30.1' W | 96        | Smith-McIntyre grab × 3 | Muddy silt                       |
| 50          | 51° 04.6' N | 06° 17.0' W | 103       | Smith-McIntyre grab × 3 | Silty mud                        |
| 51          | 51° 05.0' N | 06° 06.0' W | 96        | Smith-McIntyre grab × 3 | Mud                              |
| 52          | 51° 04.0' N | 06° 04.0' W | 96        | Agassiz trawl           | Silty mud                        |
| 53          | 51° 03.0' N | 06° 00.0' W | 92        | Otter trawl             | No data                          |
| 54          | 51° 05.8' N | 05° 54.3' W | 89        | Smith-McIntyre grab × 3 | Silty mud                        |
| 55          | 51° 05.0' N | 05° 42.3' W | 85        | Smith-McIntyre grab × 3 | Muddy sand                       |
| 56          | 51° 05.0' N | 05° 30.1' W | 87        | Smith-McIntyre grab × 3 | Fine sand                        |
| 57          | 50° 53.5' N | 09° 30.0' W | 121       | Agassiz trawl           | No data                          |
|             |             | (approx.)   |           |                         |                                  |
| 58          | 50° 53.8' N | 09° 07.8' W | 119       | Agassiz trawl           | Muddy sand, gravel, stones       |
|             |             |             | 117       | Day grab                |                                  |
| 59          | 50° 57.9' N | 08° 42.0' W | 110       | Agassiz trawl           | Mud, sand, gravel, shells        |
| 60          | 50° 50.6' N | 08° 44.8' W | 110       | Agassiz trawl           | Gravel, stones, shells           |
| 61          | 50° 51.8' N | 08° 29.3' W | 113       | Agassiz trawl           | Muddy sand                       |
|             |             |             | 113       | Day grab                |                                  |
| 62          | 50° 56.9' N | 08° 17.1' W | 102       | Agassiz trawl           | No data                          |
|             |             |             | 102       | Day grab                |                                  |
| 63          | 50° 54.1' N | 07° 53.9' W | 102       | Agassiz trawl           | Mud, small stones                |
| 64          | 50° 56.5' N | 07° 03.0' W | 93        | Agassiz trawl           | Muddy gravel, large stones       |
| 65          | 50° 55.0' N | 06° 42.0' W | 98        | Day grab × 3            | Coarse sand, stones, shells      |
| 66          | 50° 55.0' N | 06° 30.0' W | 96        | Day grab × 2            | Sand, large shells               |
| 67          | 50° 54.0' N | 06° 29.0' W | 96        | Agassiz trawl           | No data                          |
| 68          | 50° 55.2' N | 06° 18.0' W | 98        | Smith-McIntyre grab × 3 | Muddy silt                       |
| 69          | 50° 42.2' N | 09° 17.8' W | 126       | Agassiz trawl           | No data                          |
| 70          | 50° 42.2' N | 08° 51.8' W | 106       | Agassiz trawl           | Medium sand                      |
|             |             |             | 110       | Day grab                |                                  |
| 71          | 50° 45.5' N | 07° 43.1' W | 106       | Agassiz trawl           | Mud                              |
| 72          | 50° 45.0' N | 07° 17.5' W | 96        | Agassiz trawl           | Muddy sand, shells               |
| 73          | 50° 45.1' N | 07° 05.0' W | 101       | Agassiz trawl           | Muddy sand, large stones, shells |
| 74          | 50° 45.0' N | 06° 53.5' W | 99        | Agassiz trawl           | Muddy sand, stones, shells       |
|             |             |             | 99        | Day grab                |                                  |
| 75          | 50° 45.0' N | 06° 42.0' W | 97        | Day grab × 3            | Muddy sand, shells               |
| 76          | 50° 45.0' N | 06° 30.0' W | 96        | Day grab × 3            | Muddy sand, shells               |
| 77          | 50° 35.1' N | 09° 08.4' W | 95        | Agassiz trawl           | Sand, shells                     |
|             |             |             | 91        | Day grab                |                                  |
| 78          | 50° 33.0' N | 08° 39.0' W | 115       | Agassiz trawl           | Muddy sand                       |
|             |             |             | 115       | Day grab × 2            |                                  |
| 79          | 50° 39.2' N | 08° 25.2' W | 117       | Agassiz trawl           | Sandy mud                        |
| 80          | 50° 33.4' N | 08° 07.1' W | 85        | Agassiz trawl           | Medium sand                      |
|             |             |             | 90        | Rock dredge             |                                  |
| 81          | 50° 33.8' N | 07° 51.3' W | 116       | Agassiz trawl           | Muddy sand                       |
| 82          | 50° 35.4' N | 06° 42.0' W | 100       | Day grab × 3            | Muddy sand, shells               |
| 83          | 50° 34.8' N | 06° 30.4' W | 98        | Day grab × 3            | Muddy sand, shells               |
| 84          | 50° 34.7' N | 06° 29.8' W | 98        | Agassiz trawl           | No data                          |
| 85          | 50° 25.0' N | 08° 56.0' W | 99        | Agassiz trawl           | Medium sand                      |
|             |             |             | 99        | Day grab                |                                  |
| 86          | 50° 28.2' N | 08° 20.0' W | 78        | Agassiz trawl           | Medium sand                      |
|             | 50° 28.1' N | 08° 18.9' W | 77        | Agassiz trawl           |                                  |
|             |             |             | 81        | Rock dredge             |                                  |



OFFSHORE MOLLUSCA OF CELTIC SEA  
SYSTEMATIC LIST

*Notes*

1) *Nomenclature*. The nomenclature follows various authors: Caudofoveata (Salvini-Plawen, 1975); Solenogastres (Salvini-Plawen, 1971); prosobranch Gastropoda (Graham, 1971); opisthobranch Gastropoda (Thompson and Brown, 1976) and Bivalvia (Tebble, 1976).

2) *Species records*. The station(s) at which a species was found is listed after the name and authority of each species. Each station record includes a code to the type of sampling gear used and an abundance rating for the species. Gear codes used are 'T', 'D' or 'G', indicating trawl, dredge and grab respectively. Details of the exact type of gear used are given in Table 1. Abundance ratings used are '(R)' indicating a single specimen found in a sample, '(O)' between 2 and 10 individuals in a sample, and '(A)' indicating more than 11 individuals were present. This abundance scale is purely arbitrary and is included to give some idea of the relative abundance of species at a particular station. Comparisons of the abundance of species between stations should not be made.

Where, for example, 2 grabs were taken at a site and a species was present in both samples, both records are indicated: thus, for example, 7D(O), 7D(O) would not represent a misprint.

An asterisk in front of a species name indicates that the species is not recorded in either the Plymouth or the Isle of Man faunas (M.B.A., 1957; Bruce *et al.*, 1963).

Where the records of a species warrant some discussion, this is included directly after the species station list.

PHYLUM MOLLUSCA

CLASS CAUDOFOVEATA

Chaetodermatidae

*Chaetoderma nitidulum* Lovén. 18D(O), 19D(O), 25D(R), 28D(O), 40D(R), 41D(O), 45G(R), 51G(R), 54G(R), 54G(O), 59T(R), 68G(R), 70T(R).

The taxonomy of the caudofoveate molluscs has only recently been elucidated, and a monograph on the north-east Atlantic species has been published (Salvini-Plawen, 1975). Specimens from this survey have been confirmed by Dr. Salvini-Plawen and represent a significant southerly extension of authentic records of the species. *C. nitidulum* has been recorded off the Isle of Man (Bruce *et al.*, 1963), and whilst it is likely that *C. nitidulum* is present in that area, Salvini-Plawen (1975) questions the records in Bruce *et al.* (1963), and a '*C. nitidulum*' examined by him from the Isle of Man was the caudofoveate *Scutopus ventrolineatus* Salvini-Plawen. More modern records are urgently needed to establish the ranges of the British caudofoveate species.

CLASS SOLENOGASTRES

Lepidomeniidae

*Nematomenia banyulensis* (Pruvot). 2T(A).

Proneomeniidae

*Rhopalomenia* (*Proneomenia*) *aglaopheniae* (Kowalevsky and Marion). 14T(O), 18T(A), 18D(R), 19T(R), 20T(R), 25T(O), 36T(O), 37T(R), 40T(R), 47T(O).

This species was always found coiled round the stem of the hydroid *Thecocarpus myriophyllum* (L.).

Neomeniidae

*Neomenia carinata* Tullberg. 2T(R), 4D(R), 20T(R), 70G(R), 77T(R).

Pararrhopaliidae

\**Eleutheromenia* (*Paramenia*) ?*sierra* (Pruvot). 2T(R).

Regrettably only a single damaged specimen of this species was found and it has not been possible to make a full identification. The shape of the body, the dorsal keel and the spicules correspond closely to the figures of *E. sierra* in Pruvot (1891, as *Paramenia sierra*) which has previously only been recorded from the Mediterranean. Although identification to species requires further specimens, the genus is added to the British fauna.

CLASS POLYPLACOPHORA

Lepidochitonidae

*Lepidochitona cinereus* (L.). 47T(R), 69T(R).

Unidentified chitons were widely distributed in the Celtic Sea. Mr. G. H. Brown kindly identified *L. cinereus*.



## CLASS GASTROPODA

## SUBCLASS PROSOBRANCHIA

## Fissurellidae

\**Emarginula crassa* Sowerby. 84T(R).

A northern species 'in Britain appears to be limited to the west coast of Scotland and the Northern Isles; also recorded from south-west Ireland and Antrim.' (Fretter and Graham, 1976).

*Emarginula reticulata* Forbes and Hanley. 9D(R), 64T(O), 73T(R), 74T(R).

## Lepetidae

*Propilidium exiguum* (Thompson). 22T(R), 24T(O), 35T(O), 42T(O), 43T(O), 70T(R).

*Lepeta fulva* (Müller). 73T(O), 74T(O).

## Trochidae

*Gibbula tumida* (Montagu). 2T(O), 9D(O), 11T(R), 15T(O), 16T(O).

*Cantharidus montagui* (Wood). 17T(R).

*Calliostoma zizyphinum* (L.). 1T(O).

*Calliostoma papillosum* (da Costa). 1T(O), 2T(O), 43T(R).

\**Calliostoma occidentale* (Mighels). 2T(R), 67T(R), 73T(R).

This species is described as a boreal form found on both sides of the Atlantic and 'off British coasts, north of the Humber on the east but not on western British or any Irish coasts.' (Fretter and Graham, 1977). The identity of the specimens from the Celtic Sea has been confirmed by Dr. V. Fretter and these records significantly extend the known southerly range of the species.

## Turbinidae

*Tricolia pullus* (L.). 1T(R).

## Lacunidae

\**Lacuna crassior* Montagu. 1T(O).

This is the least common species of *Lacuna* and is regarded as a northern form (Graham, 1971.)

## Rissoidae

*Alvania punctura* (Montagu). 1T(R), 73T(R).

*Rissoa inconspicua* Alder. 2T(O), 7T(R).

*Cingula proxima* (Forbes and Hanley). 82G(R).

*Cingula ?vitrea* (Montagu). 27T(R).

## Turritellidae

*Turritella communis* Risso. 13T(O), 18T(A), 20T(R), 22T(R), 23T(R), 24T(A), 25T(A), 25D(O), 28T(A), 28D(R), 30T(R), 31T(A), 35T(O), 37T(O), 38T(O), 41T(A), 41D(O), 42T(A), 43T(O), 45T(O), 46T(O), 48T(O), 59T(O), 60T(O), 61T(O), 63T(A), 64T(A), 68G(R), 69T(O), 71T(O), 72T(O), 73T(R), 74T(A), 78T(A), 79T(A), 85T(R).

## Cerithiopsidae

*Cerithiopsis barleei* Jeffreys. 2T(R).

## Aporrhaidae

*Aporrhais pespelecani* (L.). 13T(R), 13D(O), 14T(R), 15T(R), 16T(O), 17T(A), 18T(O), 20T(O), 21T(A), 22T(O), 23T(O), 24T(A), 25T(O), 25D(R), 29T(A), 30T(O), 31T(A), 32T(O), 33T(O), 34T(O), 35T(A), 43T(R), 44T(O), 45T(O), 48T(O), 58T(O), 59T(R), 60T(O), 69G(R), 70T(O), 73T(O), 78T(A), 85T(O).

## Trichotropidae

## Capulidae

*Capulus ungaricus* (L.). 2T(R), 13T(R), 35T(R), 45T(R), 60T(R), 64T(R), 69T(R), 73T(O), 78T(O), 79T(O).

## Naticidae

*Natica alderi* Forbes. 1T(R), 5D(R), 16T(O), 21T(R), 30T(R), 31T(O), 44T(R), 45T(R), 59T(R), 65G(O), 68G(R), 70G(A), 79T(O), 82G(R).

*Natica montagui* Forbes. 17T(R), 18D(R), 22T(R), 23T(R), 29T(O), 30T(R), 31T(R), 33T(R), 34T(R), 40T(R), 46T(O), 50G(R), 50G(R), 52T(R), 58G(R), 60T(R), 61T(R), 64T(R), 72T(R), 74T(O), 78T(R), 79T(O), 81T(O).

## Scalidae

*Clathrus turtonis* (Turton). 18T(O), 35T(R), 36T(O), 44T(R), 46T(R), 58G(R), 60T(O), 71T(R), 74G(R), 79T(A), 82G(O).

## Euliminidae

*Eulima trifasciata* (Adams). 2T(R).

*Balcis alba* (da Costa). 18T(R), 24T(R).

*Balcis devians* (Monterosato). 18T(R).

A specimen of the crinoid *Antedon bifida* (Pennant), which is the usual host for the ectoparasitic *B. devians* (Graham, 1971), was present in the sample from station 18.

## Stiliferidae

*Pelseneeria stylifera* (Turton). 84T(O).

This species, together with several egg masses, was present on a single specimen of the echinoid *Psammechinus miliaris*



(Gmelin). *P. stylifera* has also been recorded on *P. miliaris* off Plymouth and on the echinoid *Echinus esculentus* L. elsewhere (Graham, 1971).

#### Muricidae

*Trophon muricatus* (Montagu). 2T(R), 43T(R), 73T(R).

*Ocenebra erinacea* (L.). 1T(O), 6T(R).

#### Buccinidae

*Buccinum undatum* L. 8T(R), 11T(R), 22T(R), 30T(R), 31T(R), 36T(R), 44T(R), 58T(R).

\**Buccinum humphreysianum* Bennet. 22T(O), 30T(R), 43T(R), 60T(R), 64T(R).

A rare species found from Portugal to the Shetlands and Norway (Nordsieck, 1968).

*Neptunea antiqua* (L.). 14T(R), 24T(R), 48T(R).

*Colus gracilis* (da Costa). 34T(R), 58T(O), 60T(R), 77T(R).

*Colus jeffreysianus* (Fischer). 13T(R), 20T(R), 33T(R), 59T(R), 60T(R), 64T(R).

#### Nassidae

*Nassarius incrassatus* (Ström). 2T(O), 81T(R).

#### Conidae

*Philbertia purpurea* (Montagu). 60T(R).

*Mangelia nebula* (Montagu). 34T(R).

*Mangelia brachystoma* (Philippi). 18T(O), 28D(R), 79T(R).

### SUBCLASS OPISTHOBRANCHIA

#### Pyramidellidae

*Turbonilla acuta* (Donovan). 7D(R), 7D(O).

*Turbonilla crenata* (Brown). 7D(R), 13T(R), 18T(A), 25T(O).

*Chrysallida spiralis* (Montagu). 1T(R), 6T(R).

*Odostomia unidentata* (Montagu). 7D(R), 7D(O), 7T(R), 60T(R).

*Odostomia conoidea* (Brocchi). 7D(R).

*Odostomia eulimoides* Hanley. 29T(R).

\**Menestho diaphana* (Jeffreys) (= *Odostomia perezii* Dautzenberg and Fischer). 6T(R), 60T(R).

*Menestho diaphana* is an ectoparasite of the sipunculan *Phascolion strombi* (Montagu) and the occurrence of this association has recently been recorded off Plymouth and in the Celtic Sea by Gibbs (1978). The species has been regarded as rare, but Dr. Gibbs suggests that close examination of shells inhabited by *P. strombi* will prove the species more common than was previously believed; indeed, from the Celtic Sea he records 6 specimens from one *Turritella* shell occupied by *P. strombi*. *P. strombi* was found to be widely distributed and often common in the Celtic Sea. It was found at 44 stations in the present survey, inhabiting a wide variety of shells, chiefly *Aporrhais*, *Turritella* and *Dentalium*. Every shell likely to harbour the ectoparasite was broken open, and not once was *M. diaphana* found. The commensal polychaete *Syllis cornuta* Rathke was very often present, as at station 69, where of 21 shells with *P. strombi*, 16 contained *S. cornuta*.

It is likely that during preservation, *M. diaphana* becomes detached from its host and the parasites being small, (1.0–2.5 mm shell length; Gibbs, 1978), were probably not retained by the 1 mm square mesh sieve used during this survey. Thus workers interested in the *M. diaphana*–*P. strombi* association should examine fresh material, use a smaller mesh size, or preserve the *P. strombi*-inhabited shells separately.

#### Acteonidae

*Acteon tornatilis* (L.). 19T(R), 20D(R), 41D(R), 54G(R), 78G(R), 79T(R).

#### Retusidae

*Retusa obtusa* (Montagu). 36T(R), 82G(R).

\**Retusa umbilicata* (Montagu). 18T(A).

Recorded as occurring 'all around the British Isles, usually in muddy sand'. (Thompson and Brown, 1976).

#### Scaphandridae

*Cyllichna cylindracea* (Pennant). 7D(O), 13D(R), 28D(R), 54G(R), 54G(R), 75G(R), 79T(R).

*Scaphander lignarius* (L.). 7D(O), 7D(R), 17T(R), 23T(R), 24T(O), 25D(O), 28D(R), 33T(R), 35T(R), 36T(R), 41D(R), 46T(R), 70T(O), 73T(R), 75G(R), 78T(O), 79T(O), 81T(O).

#### Pleurobranchidae

*Berthella plumula* (Montagu). 43T(R).

#### Tritoniidae

*Tritonia hombergi* Cuvier. 12T(R), 13T(O), 14T(O).

*Tritonia plebeia* Johnson. 7T(O).

#### Lomanotidae

*Lomanotus marmoratus* (Alder and Hancock). 1T(O), 2T(O), 13T(R), 25T(R).

#### Dendronotidae

*Dendronotus frondosus* (Ascanius). 12T(R).

#### Dotoidae

*Doto coronata* (Gmelin). 13T(O), 24T(R).



*Doto cuspidata* Alder and Hancock. 9D(R).

A rare species, recorded in British waters from the Shetlands and off the Isle of Man (Thompson and Brown, 1976).

*Doto fragilis* (Forbes). 2T(O), 13T(O).

*Doto pinnatifida* (Montagu). 2T(O), 7T(O), 13T(O), 24T(R), 37T(R).

Goniodorididae

*Goniodoris nodosa* (Montagu). 4G(R), 9D(O).

\**Okenia leachi* (Alder and Hancock). 48T(R).

A very rare species. The specimen was confirmed by Mr. G. H. Brown and this record is probably the first authentic record this century. Previously found off the Hebrides, Durham, Connemara and Devon (Thompson and Brown, 1976).

*Okenia* sp. 17T(R), 79T(R).

Onchidorididae

*Acanthodoris pilosa* (Müller). 1T(R), 5T(O), 34T(R).

*Onchidoris* sp. 14T(R), 18T(O), 24T(R), 34T(R), 70G(R).

Polyceridae

*Polycera quadrilineata* (Müller). 2T(R).

*Limacia clavigera* (Müller). 1T(R).

Arminidae

*Armina loveni* (Bergh). 7D(R).

An uncommon species widely distributed around the British Isles (Thompson and Brown, 1976). Also present in the sample were colonies of the sea pen *Virgularia mirabilis* O. F. Müller which is believed to be the food of this species (Brown, personal communication).

Antiopellidae

*Antiopella cristata* (Chiaje). 2T(R).

Cuthonidae

*Cuthona ?nana* (Alder and Hancock). 73T(R).

Calmididae

?*Calma glaucoides* (Alder and Hancock). 80T(O).

Nudibranchia indet. It has not been possible to identify several specimens, particularly juvenile aeolids and cuthonids.

#### CLASS SCAPHOPODA

*Dentalium entalis* Linné. 22T(R), 33T(R), 34T(O), 35T(O), 58T(R), 64T(O), 65G(R), 70G(R), 72T(R), 77T(R), 78T(R), 78G(R), 82G(R), 83G(O), 83G(O).

#### CLASS BIVALVIA

Nuculidae

*Nucula sulcata* Bronn. 19D(R), 25T(O), 26T(O), 27T(A), 27D(R), 31T(R), 37T(R), 39T(O), 40T(O), 41D(O), 42T(R), 46T(A), 52T(R), 59T(O), 61T(O), 63T(O), 75G(R), 78T(O), 79T(O), 81T(O).

*Nucula nucleus* (Linné). 1T(O), 5D(R), 13D(R), 18D(R), 29T(O), 60T(R).

*Nucula hanleyi* Winckworth. 16T(A), 17T(O), 22T(R), 23T(O), 29T(O), 33T(R), 44T(R), 45T(R), 47T(R), 58G(R), 62T(O).

*Nucula turgida* Leckenby and Marshall. 7D(O), 7D(O), 13D(A), 24T(O), 30T(O), 31T(O), 31G(O), 42T(R), 55G(O), 56G(O), 56G(O).

*Nucula tenuis* (Montagu). 26D(R), 27T(A), 27D(O), 28D(O), 38D(R), 39T(O), 40T(O), 40D(R), 51G(R).

Nuculanidae

*Nuculana minuta* (Müller). 10D(R).

Tebble (1976) reports that *Nuculana minuta* ranges from the Arctic to the English Channel, inhabiting muddy sands and gravels in water depths of 9.1–182.9 m. Although not found during his surveys of the English Channel, Holme (1966) regards the species as an 'Eastern Channel' species, i.e. a northern form with limited westerly penetration into the Channel. *N. minuta* was found at low densities (1–2 per m<sup>2</sup>) and only north of the Dogger Bank in a survey of the central North Sea (Petersen, 1977). A single specimen of *N. minuta* is reported off the Isle of Man (Bruce *et al.*, 1963), although the species is common in the Clyde Sea area with densities up to 210 per m<sup>2</sup> being recorded by Ansell and Parulekar (1978). Ansell and Parulekar (1978) found *N. minuta* together with the polychaete *Lipobranhus jeffreysi* (McIntosh), and the echinoderms *Amphiura chiajei* Forbes and *Brissopsis lyrifera* (Forbes), both in grab and trawl samples. *Lipobranhus jeffreysi* was not taken in this survey, although *Amphiura chiajei* and *Brissopsis lyrifera* were widely distributed and common on muddy sediments in depths of 82–131 m (found at 28 and 27 stations respectively). Thus it would appear that suitable substrates for colonization by *N. minuta* are not lacking in the Celtic Sea and it seems likely that the species reaches the southerly limit of its distribution in the Celtic Sea.

Glycymeridae

*Glycymeris glycymeris* (Linné). 1T(R), 4G(R), 4D(O), 4D(O), 6T(O), 6D(A), 9D(R), 13D(R), 17T(O), 45T(O).

Anomiidae

*Monia patelliformis* (L.). 1T(O), 4D(R), 5D(O).

*Monia squama* (Gmelin). 1T(O), 4T(O), 12T(O), 31T(O), 34T(R), 60T(R), 64T(O), 70T(R), 73T(O), 85T(R).



## OFFSHORE MOLLUSCA OF CELTIC SEA

*Heteranomia squamula* (L.). 1T(A), 2T(O), 5T(R), 5D(O), 6T(O), 13T(R), 16T(R), 23T(O), 30T(O), 31T(O), 43T(O), 44T(O), 58T(A), 59T(O), 60T(O), 64T(R), 69T(O), 77T(O), 79T(O).

### Mytilidae

*Mytilus edulis* L. 12T(A).

*Modiolus modiolus* (L.). 1T(A), 2T(R), 6T(R), 6D(R), 10T(R), 11T(R), 15T(R).

*Modiolus phaseolinus* (Philippi). 1T(A), 2T(O), 4G(O), 4D(R), 4D(O), 5T(A), 5D(A), 6T(A), 6D(O), 9D(A), 10T(O), 10D(A), 11T(O), 12T(O), 13T(O), 14T(O), 15T(O), 17T(A), 18T(O), 24T(R), 30T(R), 34T(R), 35T(O), 60T(O), 61G(R), 64T(O), 66G(R), 73T(A), 74T(R).

*Musculus marmoratus* (Forbes). 1T(A), 2T(R), 5T(A), 5D(O), 6T(R), 14T(R), 22T(R), 44T(R), 48T(O), 58T(R).

### Pinnidae

*Pinna fragilis* Pennant. 60T(O).

### Pectinidae

*Pecten maximus* (L.). 60T(R).

*Chlamys distorta* (da Costa). 1T(O), 2T(R).

*Chlamys opercularis* (L.). 1T(O), 2T(A), 4T(A), 7T(A), 9D(R), 10T(R), 13T(O), 14T(A), 18T(O), 18D(R), 24T(R), 25T(O), 26T(O), 36T(O), 37T(R), 43T(R), 64T(R), 81T(R).

*Chlamys tigerina* (Müller). 1T(O), 2T(O), 4T(A), 4D(R), 9D(O), 10T(R), 15T(O), 16T(A), 17T(R), 29T(O), 31T(R), 33T(O), 34T(O), 36T(A), 43T(R), 45T(O), 60T(O), 64T(O), 65G(O), 67T(R), 73T(O), 84T(O).

*Chlamys striata* (Müller). 5T(R), 48T(O), 63T(R), 64T(R), 71T(O), 74T(O).

*Similipecten similis* (Laskey). 2T(O), 13T(O), 16T(O), 17T(R), 23T(R), 29T(R), 34T(R), 35T(O), 57T(R), 58G(O), 63T(R), 65G(R), 70G(R), 73T(R), 74T(R), 79T(A).

### Astartidae

*Astarte sulcata* (da Costa). 2T(R), 11T(O), 16T(R), 21T(O), 22T(O), 29T(O), 30T(O), 31T(O), 33T(R), 34T(R), 35T(R), 36T(R), 43T(O), 44T(O), 45T(O), 47T(O), 59T(O), 60T(O), 72T(R), 73T(O).

*Astarte triangularis* (Montagu). 8D(R).

### Lucinidae

*Myrtea spinifera* (Montagu). 51G(R), 54G(R), 64T(O), 75G(R).

*Lucinoma borealis* (L.). 7D(O), 28D(O), 51G(R), 54G(R), 55G(R), 56G(O).

### Thyasiridae

*Thyasira flexuosa* (Montagu). 7D(A), 7D(A), 19D(R), 27T(O), 27D(O), 28D(A), 31G(R), 39T(O), 40T(R), 40D(R), 41D(O), 45G(R), 50G(R), 51G(O), 51G(O), 54G(O), 54G(O), 55G(O), 56G(O), 56G(O), 63T(R), 68G(O), 68G(R), 74T(R), 75G(O), 82G(R).

### Kelliidae

*Kellia suborbicularis* (Montagu). 1T(O), 5T(O), 5D(O), 6T(A), 6D(O), 10D(R), 22T(R), 60T(O), 64T(O), 73T(A).

*K. suborbicularis* was found generally in galleries in old *Arctica* or *Glycymeris* shells which had previously been bored by the sponge *Cliona celata* Grant. The bivalve *Hiattella* sp. was often also present.

### Montacutidae

*Montacuta substriata* (Montagu). 9T(O), 14T(R), 16T(A), 21T(A), 22T(O), 24T(R), 29T(A), 30T(O), 31G(R), 33T(O), 35T(O), 36T(R), 36D(O), 44T(O), 45T(R), 57T(A), 59T(A), 67T(R), 69T(O), 70T(A), 77T(O), 86T(O).

*Montacuta ferruginosa* (Montagu). 19D(O), 20D(O), 26D(O), 27T(O), 40T(O), 40D(O), 61T(O), 63T(O), 68G(O), 74G(R), 78G(R).

*Mysella bidentata* (Montagu). 7D(R), 7D(R), 19D(R), 20D(A), 28D(R), 73T(R).

### Arcticidae

*Arctica islandica* (L.). 7D(O), 7D(O), 16T(R), 17T(O), 21T(R), 48T(R), 75G(R), 80D(O).

### Cardiidae

*Acanthocardia echinata* (L.). 56G(R), 64T(O).

*Parvicardium minimum* (Philippi). 39T(O), 49G(R), 50G(R), 66G(R), 68G(O), 73T(R), 74T(R), 79T(O).

*Parvicardium ovale* (Sowerby). 1T(O), 1D(R), 2T(O).

*Parvicardium scabrum* (Philippi). 2T(R), 2G(R), 18T(A), 25D(R), 45G(R), 54G(R), 64T(R), 74T(O), 78T(R), 79T(O), 81T(O).

*Laevicardium crassum* (Gmelin). 21T(R), 29T(R), 30T(R), 45T(O).

### Veneridae

*Dosinia lupinus* (L.). 7D(O), 7D(O), 22T(R), 31T(R), 49G(R), 49G(R), 55G(R), 56G(R), 58T(R), 58G(R), 64T(R), 77G(R).

*Gafrarium minimum* (Montagu). 6D(R).

*Venus casina* L. 1D(R), 11T(R), 34T(R), 47T(R), 57T(R), 59T(O), 62T(O), 67T(O).

*Venus ovata* Pennant. 1T(R), 1D(R), 2T(O), 2G(O), 4D(R), 4D(R), 5D(R), 10D(O), 15T(O), 31T(R), 33T(R), 48T(R), 63T(R), 72T(O), 74T(R), 76G(R).

*Venus striatula* (da Costa). 7D(A), 7D(O), 13D(R), 18T(R), 18D(R), 19D(R), 23T(R), 55G(R), 56G(R), 74T(O).

*Venerupis ?rhomboides* (Pennant). 1T(R), 4D(R) (both specimens juvenile).

### Mactridae

*Mactra corallina* (L.). 3T(R).



*Spisula elliptica* (Brown). 1D(O), 8T(R), 8D(O), 9D(R), 14T(O), 15T(O), 16T(O), 17T(A), 20T(R), 21T(O), 22T(R), 23T(R), 30T(O), 31G(R), 34T(A), 35T(O), 44T(O), 45T(O), 47T(O), 57T(O), 58T(A), 59T(R), 62G(A), 73T(O), 77T(O), 83G(O), 85T(R), 86T(O), 86T(O).

A common species found around the British Isles (Tebble, 1976). Holme describes *S. elliptica* as a cold-water 'Eastern Channel' species not extending west of Plymouth in the English Channel. The above records show *S. elliptica* to have a widespread distribution in the Celtic Sea.

\**Spisula ovalis* (Sowerby). 3T(O).

#### Tellinidae

*Tellina pygmaea* Lovén. 8D(O).

\**Tellina balaustina* L. 44T(R).

The specimen of this species was identified by Mr. G. Oliver and the species is described by Tebble (1976) as a southerly form, rare in British waters.

#### Scrobiculariidae

*Abra alba* (Wood). 5D(A), 13D(O), 22T(O), 25D(R), 26D(R), 31T(O).

*Abra nitida* (Müller). 15T(R), 19D(A), 21T(O), 24T(O), 25D(O), 26T(O), 27D(O), 28T(R), 28D(O), 31G(R), 37D(R), 38D(O), 39T(A), 40T(A), 40D(A), 41D(A), 45G(O), 51G(O), 59T(O), 61T(O), 61G(O), 61G(O), 63T(R), 71T(O), 74T(R), 75G(O), 76G(R), 76G(R), 79T(A), 81T(O), 82G(R).

*Abra prismatica* (Montagu). 5D(R), 7D(A), 7D(A), 8D(A), 9D(R), 13D(O), 14T(O), 17T(R), 20D(A), 21T(O), 23T(O), 25D(R), 28D(O), 30T(O), 34T(O), 35T(O), 36D(R), 44T(O), 45T(O), 49G(R), 55G(O), 56G(O), 56G(R), 58T(O), 58G(R), 70G(O), 77G(R), 78G(O), 78G(O), 79T(A), 83G(R), 85T(O), 85G(O).

#### Gariidae

*Gari fervensis* (Gmelin). 7D(R).

*Gari depressa* (Pennant). 1T(R), 17T(O), 35T(R).

The specimens of this species were kindly identified by Ms. S. Whybrow.

*Gari costulata* (Turton). 6D(O), 9D(R), 35T(R), 49G(R), 73T(R).

#### Solecurtidae

*Solecurtus chamasolen* (da Costa). 26T(R), 31T(R), 40T(R), 46T(R), 63T(O), 74G(R).

#### Solenidae

*Cultellus pellucidus* (Pennant). 7T(O), 7D(O), 7D(O), 13D(O), 18T(A), 18D(O), 19D(A), 20D(R), 22T(O), 23T(O), 24T(A), 25T(A), 25D(A), 27T(O), 28T(O), 28D(O), 30T(O), 31T(O), 31G(O), 32T(O), 34T(R), 35T(O), 38T(R), 38D(R), 39T(O), 40T(R), 41T(O), 41D(O), 42T(O), 45G(O), 46T(A), 49G(R), 54G(R), 55G(R), 56G(R), 58T(R), 59T(O), 61T(O), 61G(O), 61G(O), 63T(A), 64T(O), 66G(R), 68G(R), 68G(R), 69T(R), 71T(O), 72T(A), 74T(A), 74G(O), 75G(O), 78T(A), 78G(O), 78G(A), 79T(A), 81T(A), 82G(O), 83G(O), 85G(R).

#### Myacidae

*Sphenia binghami* Turton. 1T(O), 2T(O), 4D(R).

This species has been recorded as widely occurring and common in the Bristol Channel (Warwick and Davies, 1977). In the present survey it was only found in small numbers in the St. George's Channel. The reasons for its apparent rarity in the Celtic Sea are not clear. *S. binghami* appears to occupy similar habitats to the bivalve *Hiattella* sp. (Tebble, 1976) and the latter species is both common and widely distributed in the survey area.

*Corbula gibba* (Olivi). 7D(O), 7D(O), 17T(R), 18T(A), 19D(O), 22T(R), 24T(O), 25D(R), 27T(R), 30T(R), 31T(R), 35T(O), 40D(R), 45G(O), 46T(O), 49G(R), 51G(R), 59T(O), 63T(O), 64T(O), 68G(R), 68G(R), 69T(R), 72T(O), 74T(O), 74G(O), 76G(R), 78T(O), 79T(A), 81T(O), 82G(R).

#### Hiattellidae

*Hiattella* sp. 1T(A), 2T(O), 4T(R), 4D(R), 5T(O), 5D(O), 6T(O), 6D(O), 7T(O), 8T(R), 9D(R), 10D(O), 11T(O), 12T(R), 13T(O), 14T(A), 15T(O), 18T(O), 21T(O), 22T(O), 24T(A), 25T(O), 28T(O), 29T(O), 30T(A), 31T(O), 32T(O), 34T(R), 35T(O), 36T(O), 37T(R), 38T(R), 39T(A), 41D(R), 42T(O), 43T(O), 44T(O), 45T(O), 46T(R), 48T(A), 59T(O), 60T(O), 62T(R), 63T(O), 64T(O), 68G(O), 69T(A), 70T(O), 71T(O), 72T(R), 73T(A), 74T(O), 77T(O), 78T(A), 79T(O), 80T(O), 81T(O).

Tebble (1976) and Petersen (1977) both regard the taxonomy of the species of *Hiattella* to require further investigation before complete identifications can be made. *Hiattella* sp. is widely distributed in the Celtic Sea and the species seems largely independent of sediment type, provided that suitable substrates for attachment are present (e.g. dead shells and hydroid holdfasts).

\**Saxicavella jeffreysi* Winckworth. 55T(R).

Found at scattered localities around the British Isles (Tebble, 1976). Described by Holme (1966) as a cold-water 'Eastern Channel' species not extending west of Plymouth in the English Channel.

#### Laternulidae

*Cochlodesma praetenue* (Pulteney). 8D(R), 35T(R), 70G(R).

#### Thraciidae

*Thracia villosiuscula* (Macgillivray). 34T(R), 48T(R).

*Thracia convexa* (Wood). 40T(R), 45G(R).

#### Lyonsiidae

*Lyonsia norwegica* (Gmelin). 2G(O), 24T(R), 25D(R), 63T(R), 72T(R), 74T(O), 79T(R).



## Pandoridae

*Pandora pinna* (Montagu). 18T(O), 23T(R), 29T(R), 48T(R), 54G(R), 59T(R), 63T(R), 64T(O), 69G(R), 72T(O), 73T(R), 74T(R), 78T(O), 79T(O).

## Cuspidariidae

\**Cuspidaria cuspidata* (Olivi). 34T(R), 64T(R), 72T(R).

## CLASS CEPHALOPODA

## Sepiolidae

*Sepiola ?atlantica* d'Orbigny. 4T(R), 7T(O), 18T(O), 25T(R), 42T(R), 64T(R), 80T(R), 84T(R).

## Octopodidae

*Eledone cirrhosa* (Lamarck). 59T(R), 78T(R).

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# THE TORNATINIDAE AND RETUSIDAE OF THE ARABIAN GULF

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(Read before the Society, 21 October 1978)

*Abstract:* This paper discusses the Tornatinidae and Retusidae of the Arabian Gulf. Lectotypes of *Tornatina persiana* Smith and '*Tornatina*' *inconspicua* H. Adams are selected and described. The generic positions of *Tornatina persiana* and *T. involuta* (Nevill and Nevill) are established for the first time and a new species, *Retusa tarutana*, is described. This latter is similar in shell shape to *R. obtusata* (Montagu), but is smaller, the gizzard plates are more pointed and the apical whorls are heterostrophic.

For the purposes of this paper the Arabian Gulf, or the Persian Gulf as it is otherwise known, is taken to be the area of water within the Gulf southwards and eastwards of its northern extremities in Kuwait, Iraq and Iran, to an imaginary line across the Straits of Hormuz from the tip of the Mussandam Peninsula to the town of Minab on the Iranian mainland (see Smythe, 1979, fig. 1).

Only the genera *Tornatina* and *Retusa* are dealt with here due to lack of knowledge of the animals of related genera from this area, as yet unidentified by the author.

In trying to establish the identity of species from the area of this paper much research has been done and material examined not only from the British Museum, Natural History (BMNH) and the National Museum of Wales (NMW), but also from the Cambridge University Zoology Museum (CUZM), the Royal Scottish Museum (RSM) and the Muséum Nationale d'Histoire Naturelle, Paris (MNHN). Much helpful information and advice was given by Dr. E. du Bois Reymond Marcus.

Marcus (1977) points out that *Acteocina* Gray was introduced for the fossil *A. wetherelli* and whether this was a *Tornatina* or a *Retusa* cannot be established as it is impossible to assign species correctly to these genera on shell shape alone. Examination of the gizzard plates, radula, if present, and sometimes the genitalia, is necessary. Therefore the next available name, *Tornatina*, should be used instead of *Acteocina*. This genus has a radula and the gizzard plates may or may not be equal in size and shape. *Retusa* has no radula and the gizzard plates are equal and covered with warty protuberences.

In the species from the Arabian Gulf consistent characters of the shells of a species appear to be shoulder and sutural detail, but these offer no clue to the correct genus. Within a species, spire height and the degree of involution of the apex vary considerably, sculpture is only moderately consistent in live-collected or fresh specimens, and shape varies from juvenile to adult.

Species which have been recorded from the Arabian Gulf (all of which were assigned to genera by the authors on shell characters alone) are:—

*Retusa nitida* A. Adams  
*R. pellyi* Smith

}

Both subsequently amended to *Cylichna* by their authors and not considered here as they do not appear to belong to either *Tornatina* or *Retusa*.



*R. omanensis* Melvill and Standen, 1903 (Biggs, 1973, record)

*R. turrigera* Melvill, 1910 (Mussandam. Also in MNHN from Linjah)

*Tornatina townsendi* Melvill, 1898 (Persian Gulf, 'Occasional')

*T. crithodes* Melvill and Standen, 1901 (Linjah)

*T. zoe* Melvill and Standen, 1901 (Galig)

*T. inconspicua* H. Adams, 1972 (Gais Island)

*T. persiana* Smith, 1872 (Col. Pelly collection, BMNH)

'*Retusa*' *turrigera* and '*Tornatina*' *zoe* appear to be distinctive in shape, but no live material has been available for study and no other records have been found.

*Retusa truncatula* (Brugière) occurs frequently in shell sand in all the areas within the Gulf which I have studied (including Bahrain, Saudi Arabia, Kuwait and various localities on the Iranian coast) and it is strange that no record of its occurrence seems to have been published hitherto.

#### SPECIES WHICH HAVE BEEN THE SUBJECT OF SPECIAL STUDY

##### 1. '*Tornatina*' *inconspicua* H. Adams, 1872.

1872 *Tornatina inconspicua* H. Adams: 11, pl. 3, fig. 12.

1901 *Tornatina inconspicua* A. Adams (sic), Melvill and Standen: 453.

1903 *Retusa omanensis* Melvill and Standen: 321, pl. 33, fig. 19.

1928 *Retusa omanensis* Melvill and Standen, Melvill: 112.

1973 *Retusa omanensis* Melvill and Standen, Biggs: 373.

The nine syntypes of this species are in the R. McAndrew collection, CUZM. A lectotype is selected here and illustrated (Plate 4, fig. 3). As no animal has been available for study it has not been possible to establish the correct genus for this species.

*Description of lectotype.* Shell cylindrical, rounded below, shoulders sloping inwards at an angle of about 45°, suture channelled. Colour white. Surface of upper part of last whorl finely longitudinally striate along the lines of growth and following the curve of the lip, the lower third more strongly spirally striate. Outer lip thin, curved; parietal callus weak; columella strongly folded and grooved in the umbilical region. Protoconch heterostrophic, almost covered by the succeeding whorl. Spire low. Total height 2.85 mm, width 1.50 mm.

*Discussion.* Shells of this species show much variation in spire height and the degree of plication of the columella and callosity of the inner lip. In the CUZM collections is a set of six specimens with the protoconch completely buried in the succeeding whorls, but this character is not uncommon in these genera. Fresh shells are translucent and milky white. The striae may be faint or absent in dead shells due to abrasion.

Examination of the holotype of '*Retusa*' *omanensis* Melvill and Standen in the BMNH collections shows this species to be a flat-topped form of '*T.*' *inconspicua*.

*Known distribution.* Red Sea (Cooke, 1885, p. 130; Lamy, 1938, p. 86). Persian Gulf [probably Bushire] 14 fathoms (Pelly material, BMNH), Bombay, Kais (Melvill and Standen, 1901, p. 453). Charbar (Melvill, 1928, p. 112). Basra (Hudson, Eames and Wilkins, 1957, pp. 397, 399). Abu Dhabi (Biggs, 1973, p. 373). Tarut Bay, Saudi Arabia, alive (personal communication, Mrs. L. Johansen. Unfortunately these specimens could not be obtained for study to establish the correct genus.)



2. *Tornatina involuta* (Nevill and Nevill, 1871)

1871 *Cylichna involuta* Nevill and Nevill: 3.

Originally described from the collection of Henry Nevill, the holotype is in the care of the Zoological Survey of India, Calcutta. Two specimens from the Henry Nevill collection, NMW, are figured (Plate 4, figs. 4–6, 10). The dimensions are 7.00 mm by 2.75 mm and 5.95 mm by 2.25 mm.

This species varies even more markedly than other members of these genera. Younger specimens are more cylindrical than older ones which develop a curved outline somewhat reminiscent of *T. olivaeformis* Issel and *T. fusiformis* A. Adams. Fresh specimens have a creamy periostracum with chestnut lines. *T. crithodes*, which was described as a new species on the periostracal character, is almost certainly a synonym. *T. townsendi* is also probably the same species, although examination of live collected material is needed before coming to a definite conclusion. The suture is very deeply and angularly channelled, the columella plicate and there is no umbilicus.

Gizzard plates of a specimen collected from under a stone in a rocky channel at Ras Ushariq, Kuwait, in November 1975 by Mrs. B. Glayzer, are illustrated (Plate 4, fig. 11). The two paired plates show an affinity with those of *T. gaimardi* Finlay (Marcus, 1977, fig. 6): the third smaller plate can be seen between the larger ones. The characters of these plates indicate that this species must be placed in *Tornatina*, but no radula (which may be very small) was found.

The type locality is Ceylon (Sri Lanka) and the authors record it also from Bombay and Penang. It occurs in the Red Sea (Biggs and Smythe collections) and at Karachi (Melvill). It has been found in shell sand in all the localities that I have studied in the Arabian Gulf and live specimens have been collected in Kuwait and in Saudi Arabia (personal communication, Mrs. Johansen).

3. *Tornatina persiana* Smith, 1872.

1872 *Tornatina persiana* Smith: 354 (pars).

*Original description:* *T. testa minutissima, breviter, cylindracea, alba, incrementi lineis curvatis rugosa; anfract. 3, primus ex tuberculo magno constat, caeteri superius lira magna rotundata circumcincti; sutura depressa; apertura latiuscula, brevior quam anfractus ultimis, basi sensim dilatata, columella brevis, incrassata, haud torta.*

(Shell very small, shortly cylindrical, white, growth lines curved coarsely, three whorls, from the first of which a large tubercle stands up, the others are encircled by a deep rounded furrow; the suture is depressed; the aperture is narrow, shorter than the last whorl, widening at the base, the columella is short, thick and not twisted.)

Twelve syntypes of *T. persiana* are in the BMNH collections. They consist of five specimens of one species, five specimens of another, and two specimens which cannot be assigned to any species because of their bad condition. All the shells are very small, in poor condition, and appear to be sub-fossil with a deposit cemented within the apertures.

The large apex and furrowed shoulders have been selected as the most important characters of Smith's description and the name, *T. persiana*, is here restricted to those five syntypes showing these characteristics. The others are described below as *Retusa tarutana* sp. nov.

*Description of the lectotype:* Shell very small, probably juvenile, white, cylindrical, rounded below. The shoulder of each whorl is stepped or furrowed, giving the impression of a double shoulder. Suture marked, but not channelled. Spire moderately elevated, protoconch heterostrophic, protruding above the first dextral whorl. Aperture narrow above, wider below. Outer lip thin. Columella thickened, not umbilicate. Shell striate in the lines of growth which are slightly curved. Height 1.247 mm, width 0.682 mm. Lectotype registered BMNH 1872. 3.20.8/1 (Plate 4, figs. 7–8).



*Additional information:* Adult shells are of about four whorls, excluding the protoconch. The outer lip is curved, thin, projecting forward and free from the body whorl at the suture. The inner lip has a thin callus. The columella is thickened, sometimes slightly twisted; there is a small groove in the umbilical position, but the shell is not umbilicate. There is no periostracum. Fresh shells are milky white and translucent. Spire height varies considerably from almost flat to quite elevated and the protoconch, though usually upstanding, is sometimes almost buried. Adults measure about 2.60 mm in height.

The gizzard plates of a live animal, collected by Mrs. Glayzer at Ras Ushariq with the preceding species, are illustrated (Plate 4, fig. 9). The gizzard plates are simple, slightly capped and of equal size. The radula was very small: it was seen, but lost in processing (it most probably disintegrated). However, details are sufficient to decide on the correct genus.

This species is common in shell sand throughout the Gulf and has also been collected alive in Saudi Arabia (Mrs. Johansen).

#### 4. *Retusa tarutana* sp. nov.

1872 *Tornatina persiana* Smith: 354 (pars).

1979 *Retusa* sp. nov. Smythe: 69.

The remaining five syntypes of *T. persiana* do not appear to have been described before. I propose to name them *Retusa tarutana* after my type locality.

*Description of the Holotype:* Shell cylindrical, rounded below; spire slightly elevated; protoconch heterostrophic, partly buried in the succeeding whorl. The whorls are rounded at the shoulders, meeting the preceding whorl at an angle a little greater than 90°. Suture clearly defined, but not channelled. The shell consists of 4½ whorls, including the protoconch. It is fragile, translucent, milky white and finely striate following the lines of growth, some of the striate becoming coarser at the curve of the shoulder. Aperture narrow, wider below; outer lip thin, sinuate, projecting forward and free of the body whorl at the suture. Columella weakly twisted, with no groove in the umbilical position. Height 2.53 mm, width 1.40 mm. Registered BMNH 1976154. Plate 4, figs. 1–2.

The spire height of a paratype (NMW) is lower than that of the holotype, barely projecting above the top of the body whorl. There is a thin film on the parietal lip. Height 2.20 mm, width 1.20 mm. Accession number 77.15.Z. Plate 4, fig. 12.

*Gizzard plates:* A specimen from the type locality was dissected and the gizzard plates are figured in Plate 4, fig. 13. They are typically retusid, having brown, warty protuberances. They differ from those of *R. obtusa* (Montagu) by being more pointed in outline and in having a brown

Plate 4 (opposite).

Figs. 1–2. *Retusa tarutana* sp. nov. Holotype (BMNH 1976154) × 20.

Fig. 3. '*Tornatina*' *inconspicua* H. Adams. Lectotype (CUMZ) × 20.

Figs. 4, 10. *Tornatina involuta* G. and H. Nevill. (Nevill coll., NMW) × 10.

Figs. 5–6. *Tornatina involuta* G. and H. Nevill. (Nevill coll. NMW) × 10.

Figs. 7–8. *Tornatina persiana* Smith. Lectotype (BMNH 1872.3.20.8/1) × 20.

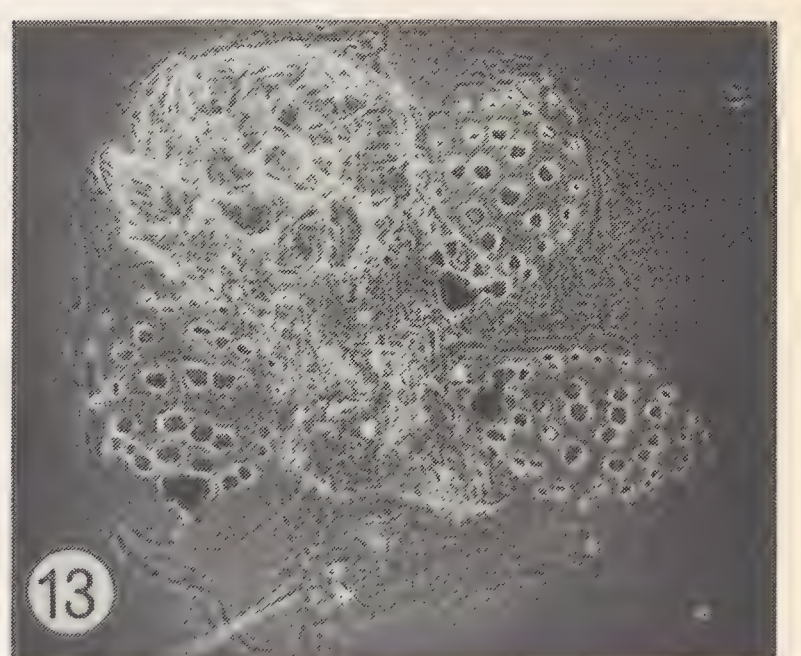
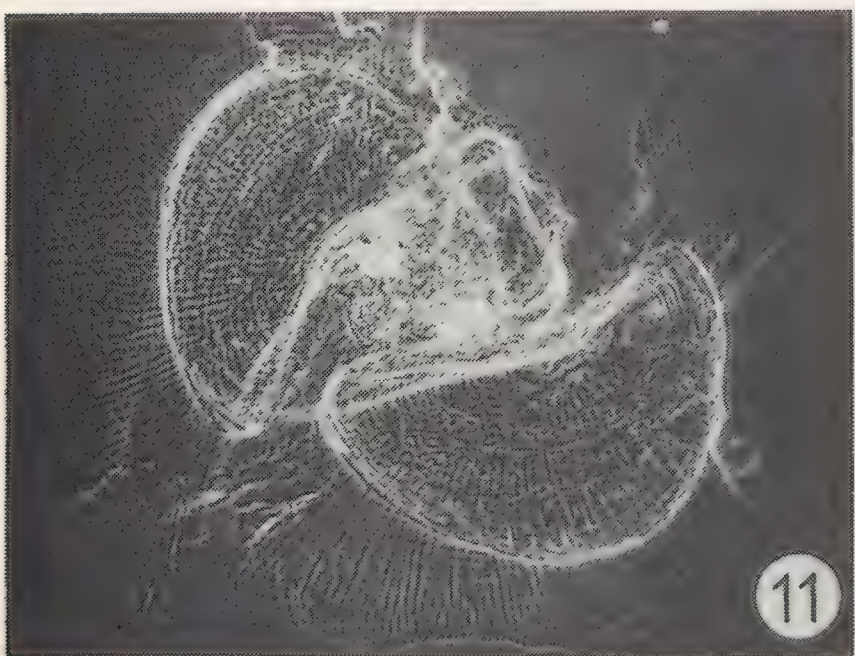
Fig. 9. Gizzard plates of *T. persiana* Smith (NMW) × 60.

Fig. 11. Gizzard plates of *T. involuta* G. and H. Nevill. (NMW) × 60.

Fig. 12. *Retusa tarutana* sp. nov. Paratype (NMW) × 20.

Fig. 13. Gizzard plates of *R. tarutana* sp. nov. (NMW) × 60.











spot at the point; also the brown 'warts' are more evenly distributed. These gizzard plates and those of the two preceding species discussed, are deposited in the National Museum of Wales.

In shell shape this new species resembles *R. obtusa*, however the latter does not have an heterostrophic larval shell and differs in the details of the gizzard plates.

*Type locality:* Dredged off Sandy Hook, Tarut Bay, Saudi Arabia, on 12 October 1974 at 4 m, by a team working under the direction of Dr. John Burchard of the Marine Biological Laboratory, Dhahran, Saudi Arabia. Molluscs sorted out from the marine algae by Mrs. Lorraine Johansen of the Laboratory. The specimens now described were presented to me by Mrs. Johansen, with the permission of Dr. Burchard, for the purposes of study. I have named them after the type locality, as this is the only locality from which I have live-collected material.

*Distribution of R. tarutana:* This species appears to be common in shell sand throughout the Arabian Gulf. I have examined material from Kuwait, Hormuz, Bushire and Abu Hayl (United Arab Emirates) in which it occurs, and I have also seen unnamed specimens from Perim Islands and from Dohar, which are in the collections of the MNHN, Paris.

#### ACKNOWLEDGEMENTS

Dissection of the three live-collected specimens discussed above was done by Dr. Vera Fretter and the gizzard plates were mounted by Dr. June E. Chatfield. The micro-photographs of the gizzard plates and the photographs of *T. involuta* and the paratype of *R. tarutana* were taken by Mr. Erick Broadbent, of the National Museum of Wales. The photographs of the lectotype of *T. persiana* and the holotype of *R. tarutana* were taken by staff of the British Museum, Natural History—the latter by Mr. Paul Richens. The photograph of the lectotype of '*T. inconspicua*' is by courtesy of the Zoological Museum, Cambridge University. Dr. Eveline Marcus gave much advice and guidance. Without the generous help of these people this paper could not have been written and I am deeply indebted to them.

I am also grateful to Major M. D. Gallagher, Mr. and Mrs. D. Glayzer and Mrs. Lorraine Johansen for specimens; to the staff of the British Museum, Natural History, the National Museum of Wales and the Department of Malacology, Institut Royal des Sciences Naturelles, Brussels for help; to the Museum Nationale d'Histoire Naturelle, the National Museum of Wales, the Royal Scottish Museum and the Zoology Museum, Cambridge, for the loan of material.

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*CATINELLA ARENARIA*  
(BOUCHARD-CHANTEREUX) AND  
*VERTIGO GEYERI* LINDHOLM, FROM A  
BASE-RICH FEN IN NORTH-WEST ENGLAND

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*Abstract:* *Catinella arenaria* and *Vertigo geyeri* have been found alive in a base-rich fen near Orton, Cumbria, England. This site, which is the first British locality for living *V. geyeri* and the second for living *C. arenaria*, resembles the Irish fens where both *C. arenaria* and *V. geyeri* can be found, rather than the British site for *C. arenaria* at Braunton Burrows, Devon.

*Catinella arenaria* (Bouchard-Chantereux) and *Vertigo geyeri* Lindholm are molluscs of local occurrence in Europe (Ehrmann, 1933; Zilch and Jaeckel, 1962; Waldén, 1966). Within the British Isles, *Catinella* and *V. geyeri* are known from calcareous fens in central Ireland (Stelfox, 1925; Phillips, 1935; Norris and Pickrell, 1972), where they are often associated with each other (Phillips, MS). In Britain *Catinella* occurs at Braunton Burrows, Devon (Boycott, 1921; Baker, 1965), whereas *V. geyeri* was not known to occur, alive, in Britain. Several of the Irish fen sites have been destroyed by, or are under threat of, drainage (Norris and Pickrell, 1972) so that it is particularly pleasing to be able to report the presence of living *Catinella arenaria* and *Vertigo geyeri* in the Orton area of the Cumbrian Pennines.

The site consists of a calcareous fen, approximately one mile northwest of Sunbiggin Tarn, Orton (Grid reference NY6707). The vegetation of the area has been described in some detail by Holdgate (1955a and b), who also gives a brief description of the geology of the site; the full data need not be presented here, but briefly the site consists of a calcareous fen developed in a shallow depression in moorland at an elevation of 250 m., watered by calcareous springs; tufaceous deposits are evident around many of these springs. *Vertigo geyeri* was found where there was a good growth of small *Carex* species (*C. lepidocarpa* Tausch, *C. hostiana* DC., *C. panicea* Linn., *C. dioica* Linn.), *Eleocharis quinqueflora* Schwarz and *Schoenus nigricans* Linn., by examining the lower leaves and stems of these plants after removal from the field. A pH of ca. 8.5 was determined for the wet soil from such a site. *Catinella arenaria* was found on a subsequent visit to the site, in association with *Vertigo geyeri*, in a rather more open habitat where bare mud and tufaceous deposits were particularly evident. Molluscs found with *Catinella arenaria* and *Vertigo geyeri* at Sunbiggin were:—*Carychium minimum* Müll., *C. tridentatum* (Risso), *Oxyloma pfeifferi* (Rossm.), *Cochlicopa lubrica* (Müll.), *Columella edentula* (Drap.), *Vertigo antivertigo* (Drap.), *V. substriata* (Jeffreys), *V. pygmaea* (Drap.), *V. lilljeborgi* (West.), *Punctum pygmaeum* (Drap.), *Arion ater* (Linn.), *A. intermedius* Normand, *Vitrea crystallina* (Müll.), *Nesovitrea hammonis* (Ström.), *Aegopinella pura*



(Alder), *Zonitoides nitidus* (Müll.), *Deroceras laeve* (Müll.), *D. reticulatum* (Müll.), *Euconulus alderi* (Gray), *Trichia hispida* (Linn.), *Lymnaea truncatula* (Müll.), *L. peregra* (Müll.) and *Pisidium personatum* Malm, although not all these species were present at any one site.

Evidently Sunbiggin resembles the base-rich fen habitats of Ireland rather than the dune slack habitat at Braunton where *V. geyeri* does not occur. This is confirmed by the similarity of the vegetation at Sunbiggin to that of the Irish fens at Fiagh Bog (near Borrisokane, Tipperary; Phillips, 1935; Norris and Pickrell, 1972) and near Birr (Offaly; B. Coles unpublished) where both *V. geyeri* and *C. arenaria* occur.

We are investigating the distribution of *Catinella arenaria* and *Vertigo geyeri* in the Orton area in detail and hope to present our findings at a later date.

#### ACKNOWLEDGEMENTS

We would like to thank Dr. L. Lloyd-Evans for confirming the identity of *Catinella arenaria* by dissection and Drs. H. W. Waldén and M. P. Kerney for confirming the identity of *Vertigo geyeri*.

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# THE IDENTITY OF THE EUROPEAN GREENHOUSE *GULELLA* (PULMONATA: STREPTAXIDAE)

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(Read before the Society, 17 February 1979)

*Abstract:* The recent collection of a living specimen of *Gulella* in Cambridge Botanic Garden led to a further search of literature and the fact that *Gulella io* Verdcourt is the same as a species described by Degner from Liberia. Details of the radula and part of the genital anatomy of the Cambridge specimen are described; these agree remarkably well with those given by Degner. A name he proposed is, however, not available for use and *G. io* remains the correct name.

*Gulella io* was described from shells alone (Verdcourt, 1974). My initial reluctance to give it a name (Verdcourt, 1969) has proved to be well-founded. The capture of a living specimen in a hothouse at the Cambridge Botanic Garden by Dr. A. J. Rundle necessitated a survey of the literature for comparative anatomical data, during the course of which it was discovered that the shell and anatomy of *G. io* fitted exactly the description given under the name *G. devia* Connolly by Degner (1934). I regret that my lack of thoroughness led me to overlook Degner's description in a paper well-known to me. Through the kindness of Prof. Dr. Peter Kaiser, Zoologisches Institut und Zoologisches Museum, Hamburg, I have been able to examine two of the original specimens from Liberia and confirm the identity of the greenhouse snail.

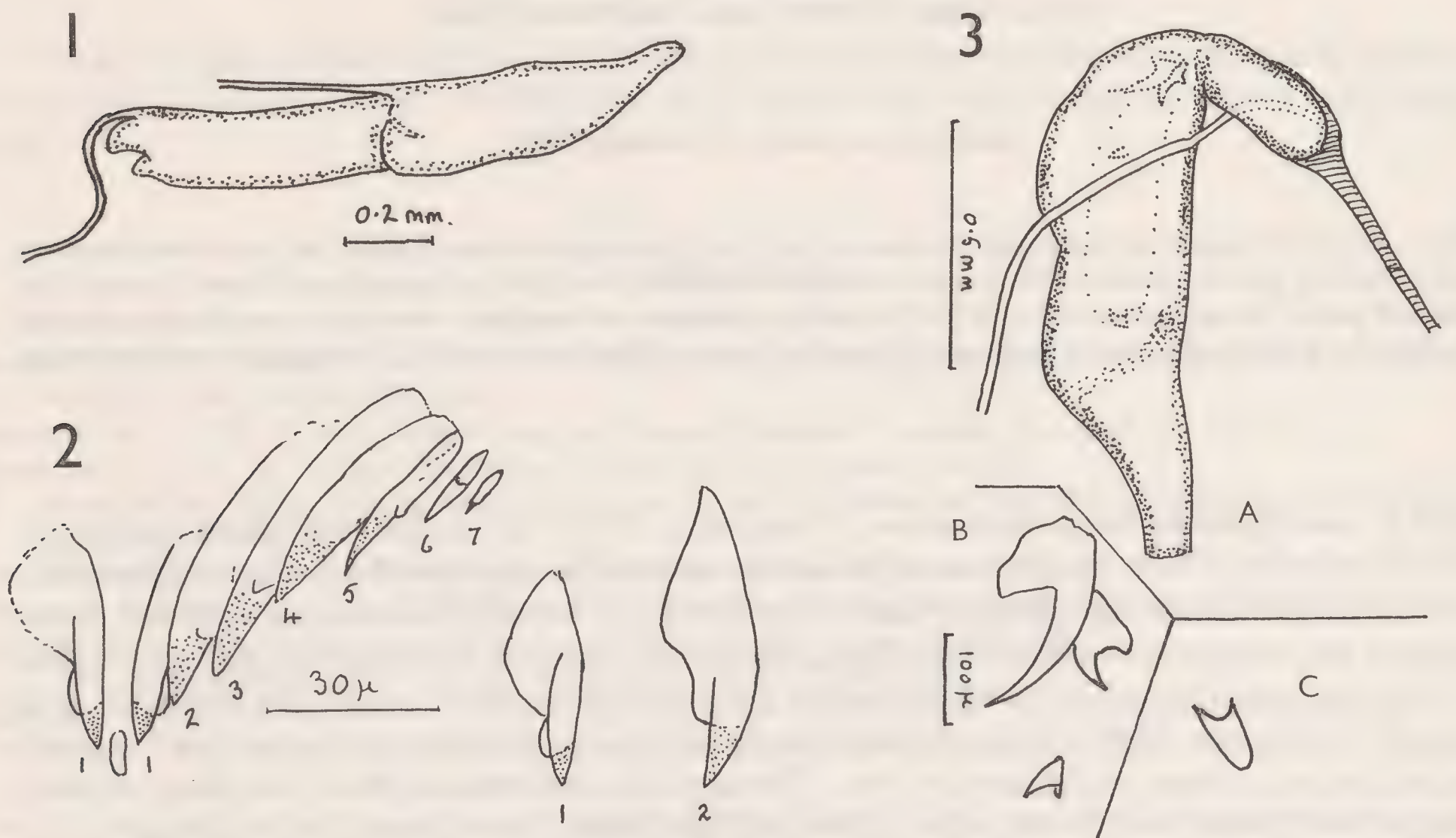
Degner's paper is a description of certain families from a large collection of snails from Liberia and, what was then, French Guinea. Descriptions of shells and considerable anatomical data are given. Degner had at first clearly considered the specimens of the species under present consideration to belong to a new species and had sent a specimen to Connolly. It is clear that Degner had at first recorded the information in his paper under the heading *G. styloidea* sp. nov. and at the last moment Connolly had identified the specimen sent to him with his own *G. devia* so that Degner had then altered his paper in page proof substituting this name and adding a footnote to explain. Apparently inadvertently he forgot to alter the caption to the drawings and these are still headed *G. styloidea*. This is not, I think, adequate to validate the name. The names *styloidea* and *devia* apply to the same species-group taxon and the former name only appeared through inadvertence and is first published as a synonym and therefore unavailable under Article 11(d) of the Zoological Code. The name is also at variance with the requirements of Article 13(a) (i) which requires a name published after 1930 to be accompanied by a statement purporting to give characters differentiating the taxon concerned. In the footnote Degner mentions the difference in the position of the parietal denticle and the unlikely occurrence of the same species in Liberia and Uganda (Mt. Elgon, 2300-3000 m). Clearly he was dubious still, but equally clearly he no longer accepted his own new species. I have already explained



(Verdcourt, 1969) how Connolly had exactly similarly misnamed Edinburgh material as *G. devia*. The formal synonymy can now be set out as follows:—

*Gulella io* Verdcourt, 1974

- 1931 *Gulella devia* Connolly: 311 (Edinburgh specimens only; *non* Connolly, 1931 *sensu stricto*).  
 1934 *Gulella styloidea* Degner: 250 sub fig. 26a, b in syn. (unavailable name).  
 1934 *Gulella devia* Degner: 250, fig. 26a, b (*non* Connolly, 1931).  
 1969 *Gulella* sp.; Verdcourt: 15, fig. 1.  
 1973 *Gulella* sp.; Verdcourt in Airy Shaw: 389.  
 1974 *Gulella io* Verdcourt: 121, fig. 1.  
 1976 *Gulella io* Verdcourt, Flasar and Kroupová: 149, fig. 1.  
 1976 *Gulella io* Verdcourt, Flasar and Kroupová: 65, fig.  
 1979 *Gulella io* Verdcourt, Kerney and Cameron: 212, fig. p. 207.



*Gulella io* Tropical Fern House, Cambridge Botanic Garden, A. J. Rundle leg. Fig. 1. Salivary gland. Fig. 2. Part of row of radula and isolated teeth. Fig. 3. A, penis showing position of spinules; B, upper spinules; C, lower spinule.

The details I obtained from the animal collected by Rundle seem worth describing for comparative purposes and also since Degner's paper will not be easily available to many collectors. The snail was handed over to me on the 17 July and maintained alive for nearly two months. Unfortunately I did not observe the death of the creature in time to preserve the body in perfect condition and the information obtainable is the poorer for that fact. It died sometime towards the end of the last week in September.

The shell measured 4.1 mm tall, 1.2 mm wide near the middle and 1.4 mm wide near the base, being of a distinctly tapering shape; there were 6 whorls visible from the front. My previous measurements for the species are 3.5–4 × 1.2–1.4 mm and Degner gives 3.4–3.7 × 1.3 mm. Unfortunately the shell had to be broken to obtain the partially desiccated animal but the aperture was retained unbroken. The process at the base of the outer lip is a nodule rather than an elongated slab. When retracted the pulmonary orifice is positioned at the top of the sinus to the outside of the parietal lamellae; during retraction the whole animal save for tip of shell appears to be bright vermilion, but this colour is entirely due to the retractor muscles, the rest of



the body being greyish white. This vermilion colour is characteristic of many species of *Gulella*, e.g. *G. bicolor* (Hutton). Outstretched, the greyish white foot measures 4 mm and the tentacles 1.5 mm. The snail moves exceptionally rapidly and its presumed carnivorous habits were tested by introducing *Discus rotundatus* of various sizes into the tube. Almost immediate interest was shown in young *Discus* and *G. io* was seen to suck mucus from inside the shell of the retracted animal but it did not persevere. Several days later this *Discus* shell was found quite empty and later still the *Gulella* had returned to it and was deeply buried inside with the protrusible mouth extended presumably mopping up the last traces of the former occupant; by 27 September several *Discus* had been eaten but large specimens were avoided.

The radula was extracted and prepared; selected teeth are shown in Fig. 2. The radula is narrow, measuring 1.75 mm long  $\times$  0.16 mm wide. It was damaged during preparation but there are at least 50 rows of teeth. There is a vestige of a central tooth but quite undifferentiated and bearing no cusps; the first lateral is smaller than the next three and only about 7 laterals are clearly visible, although there appear to be up to 11 teeth in each half row. The last 5–6 teeth are minute and of no consequence. Degner gives the formula as 12–13.0.12–13  $\times$  48–58. The salivary gland and ducts are of the form characteristic of the genus (Fig. 1). Owing to the desiccation of the animal the complete reproductive system could not be made out but the most important feature, namely the internal armature of the penis, was clearly visible after soaking in chloral hydrate and is shown in Fig. 3. The central part is yellowish in colour. At the distal end the main spinule is accompanied by a smaller one; below that is a smaller one and at the base of the yellow area is yet another small one. Degner figures a very similar armament with the two distinct overlapping upper spinules and one possible lower one and states in the footnote already mentioned that he thinks this highly characteristic ‘Penisbewaffnung’ renders immediate identification possible. Few other investigators have mentioned these spinules but Adolfo Ortiz de Zarate Lopez and Antonio Ortiz de Zarate Rocandio (1955) give a survey of the anatomy of the species occurring in Fernando Po and make especial mention of the spinules and figure those of many species, but nothing as simplified as *G. io*. Practically nothing else has been published about the comparative anatomy of small African *Gulella* species, but I suspect many of them will have a similar spinule pattern to that of *G. io*.

Finally, mention should be made of other records. A specimen was found in a hot-house in the Royal Horticultural Society’s garden at Wisley by R. P. Scase (Kerney, 1976); this specimen forms the basis of the figure in Kerney and Cameron’s field guide (1979). A. J. Rundle found shells in a flower bed in the Tropical Bird House at Regents Park Zoo and extensive additional material at the Royal Botanic Gardens Kew, namely in the Palm House (live specimens), T-Range 9A (very recently dead specimens) and Tropical Fern House (about 100 shells). No further material has turned up in the Aroid House where A. Norris found the original single specimen. D. Heppell (in litt., 1968) added some details about the specimens collected in hot-houses in the Royal Botanic Garden, Edinburgh by A. R. Waterston, now in the Royal Scottish Museum. The specimens were first submitted to J. R. le B. Tomlin who originally considered them to be *G. bicolor* (Hutton), a species to which they bear scant resemblance; Tomlin showed them to Connolly who, as has been mentioned, misidentified them with his *G. devia*. A single shell retained by Tomlin should be in the collections of the National Museum of Wales and a radula slide prepared by A. J. Peile from this specimen is in the Peile collection of streptaxid radulae in The Royal Scottish Museum.

#### ACKNOWLEDGEMENTS

I am most grateful to Dr. K. G. V. Smith and Dr. R. W. Crosskey of the Dept. of Entomology, British Museum (Nat. Hist.) for advice with the nomenclatural problem discussed above. The Cambridge material has been deposited in the Rijksmuseum, Leiden.



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# THE COLONIZATION OF NEWLY-DREDGED DRAINAGE CHANNELS ON THE PEVENSEY LEVELS (EAST SUSSEX), WITH SPECIAL REFERENCE TO GASTROPODS

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(Read before the Society, 17 February 1979)

*Abstract:* Ten newly dredged drainage channels were studied at regular intervals over several years (1969-73) to find the rate and nature of colonization by plants and animals. The process was rapid and similar in all channels, but with important differences between them.

Dense cover by floating plants, mainly *Lemna minor* and *L. polyrrhiza* was general in 4 out of 5 eastern channels, where the mean number of gastropod species per sample was 6.0 at the end of the second summer following clearance. A mean total of 11.2 gastropod species was recorded for these channels during the 2-4 year period following clearance. In 5 western channels where *Lemna trisulca*, filamentous green algae and submerged plants were dominant, the corresponding mean figures for gastropods were 7.2 and 14.6. Insect taxa were also better represented in the west, but crustaceans, arachnids, leeches and flatworms were more evenly distributed. Extensive sampling in other parts of the Levels in both recently cleared and other channels confirmed the uneven distribution of gastropods and some other species.

Out of 20 species recorded, three groups of snails were distinguished according to their frequency, abundance and geographical distribution. Opportunities for transport were important in determining the pattern of colonization, but environmental factors such as drainage pattern, extent and season of dredging, width of channel and treatment with herbicide, were probably more influential.

The information in this paper may be relevant to the siting of the proposed Nature Reserve in the Pevensy Levels announced in the National Press in October, 1977.

The classic work on the distribution of freshwater Mollusca is by Boycott (1936). He considered that favourable conditions for all species are high calcium content of the water and abundant vegetation. The water should be clean, transparent and with a moderate current. Unfavourable conditions include the presence of leaves and woody tissue, a covering of *Lemna* spp. (duckweed) or thick growths of *Elodea canadensis* (Canadian pondweed) or *Phragmites communis* (Common Reed). The beneficial influence of calcium may be over-ridden by unfavourable conditions. As one factor departs from the maximum, the number of species falls. Different species disappear according to which condition deteriorates. A high standard in one may compensate for deterioration in another. Marsh drains are described as among the richer habitats for snails. Any place is 'good' if it contains more than 20 species, or if it contains one or more exacting species such as *Bithynia leachii* (Sheppard). Ten is regarded as a good number if the water is stagnant.

Macan (1974, pp. 77-78) stresses the importance of finding out whether the community in any one place is related to the environmental conditions or whether it depends on what particular species happened to reach it. He shows the need for studies over a period of years of places that have just been created or whose population has been wiped out, to see how long it takes for the flora and fauna to become stable. He also sees the need for a series of surveys of places of the same type, for if their faunas were found to be similar, it would favour the view that



environmental conditions, not the accidents of arrival, determined the composition of the population.

On the Pevensey Levels (East Sussex, England) the dredging of drainage channels at various intervals of time removes a large proportion of the flora and fauna. Among the floating debris or on the mud banks are the remnants of the plant and animal populations which will provide the first colonists, if the environmental conditions are suitable. In some cases it was possible to make a rapid survey of the community immediately before dredging and compare it with the one that developed later. By taking 10 cleared channels and comparing the community at frequent intervals, it has been possible to examine the relative importance of environmental conditions and opportunities for transport.

### THE DRAINAGE SYSTEM OF THE PEVENSEY LEVELS

The Pevensey Levels (East Sussex) comprise all the coastal marsh-land between Bexhill and Eastbourne (Fig. 1). This region initially formed a shallow bay, since silted up and artificially drained behind a protective fringe of shingle. The drainage was started before the Roman settlement at Anderida (Pevensey) and was called the 'innings' of the Levels (Salzmann, 1910).

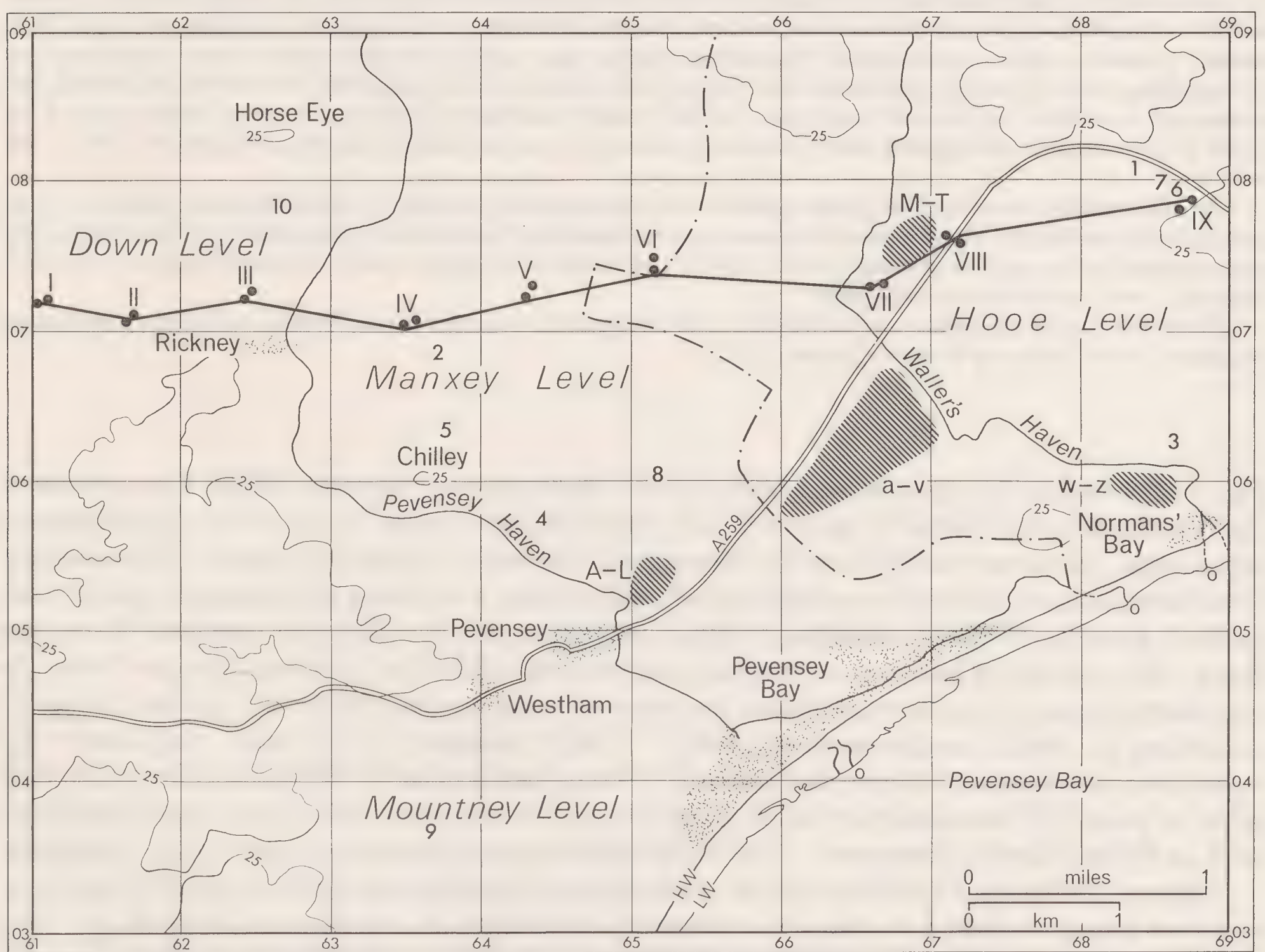


Fig. 1. Map of Pevensey Levels. ○ Outfalls in Pevensey Bay. A-T Areas sampled in 1971 (Table 6). a-z Areas sampled in 1978 (Table 8). I-IX Line of transect August, 1973 (Table 7). 1-10 Sites of main study channels. —. —. — Boundary of Hooe and Manxey Levels. Contours in feet.



The general height of the marshland is about 3 m above sea level, while halfway between Horse Eye and Rickney it sinks to a little over 1 m above sea level (see Fig. 1). The lowest ground is thus near the northern edge of the Levels, at the foot of the hills where the scouring effect of the tide in the ancient bay had the greatest influence. These parts were also some of the latest to be drained.

The water from the Levels is discharged in 3 outfalls at Pevensey Bay. The sluice gates are open in the winter to drain the fields. From about March, the gates are shut and the level of the water in the ditches rises. Until recently all drainage was by gravity flow towards the 2 main rivers, Waller's Haven and Pevensey Haven, and thence into the sea. It is being gradually changed to a pumping system for greater efficiency and to improve the grazing land for farmers. Water is continually pumped into Waller's Haven, which acts as a storage reservoir for the Eastbourne Water Board.

On each of the different Levels, the smaller channels eventually drain into a main stream or river. All water from Horseye, Down, Manxey and Mountney Levels drains into the Pevensey Haven, and water from Hooe Level drains into Waller's Haven. The flow of water is often slight and influenced on the surface by wind currents. When sluices are opened or shut, new channels are dug or the old ones dredged, the flow may be temporarily reversed or increased and this may favour rapid recolonization.

The main channels are dredged about once in 5 years by the Sussex River Authority and are treated in June each year with dalacide, to kill waterweed. The River Authority also clears other secondary channels for the farmers at less frequent intervals. The minor channels are cleared by the farmers still less frequently, sometimes not for 20 or 25 years. Altogether there are about 300 miles of waterways on the Levels.

## METHODS

Between September 1968 and March 1969, fifty channels were sampled by dips and sweeps with the net and grabs of vegetation. Lists of species were compiled and relevant environmental factors, such as depth and width of channel and evidence of recent clearance, considered. As a result it was decided to sample 10 newly dredged channels over a period of several years. The selection was made from channels cleared between Autumn 1968 and Spring 1971. As very few were cleared during this time, little element of deliberate choice was involved, except to include some cleared by the River Authority and some by farmers, some cleared in Autumn and some cleared in Spring, representing as far as possible different areas of the Levels. The Map (Fig. 1) shows the location of the channels and Table 1 summarizes some relevant facts about them.

Sampling methods were tested in 12 adjacent long-cleared channels in March and April 1971 (Table 6), in 2 widely separated channels from September 1971 to March 1972 and in 96 channels throughout the Levels on 3 consecutive days in September 1971 (Table 5). This rigorous testing of methods was necessary because of the special sampling problems. The contagious or patchy distribution of gastropods in the channels makes it difficult to choose methods which will give reliable quantitative results. If the channel is devoid of vegetation when sampling commences, the only place that the snails can colonize is the muddy bank. If there is debris from the clearance or if vegetation is already established, snails may be found among the debris and vegetation and on the bank. If the channel ends at a farm gate, whether connected by a pipe to another channel, or not, or if it is adjacent to another less recently cleared channel, more individuals and species may be found at the end section or the junction, than in mid-channel. In addition the sampling must be adequate to reveal both the seasonal and successional pattern and to obtain the other members of the fauna as well as snails.

The technique finally adopted was based on a 3 m bank sweep with a net of unbleached calico of  $2\frac{1}{2}$  l cubic capacity. Macan (1964) describes the net as 'a versatile instrument doing



TABLE 1

## Main Study Channels

| Channel                                                          | Date cleared | 1st sampled | Location<br>& level | Approx.<br>width & depth<br>after clearance |        | Type of<br>clearance |
|------------------------------------------------------------------|--------------|-------------|---------------------|---------------------------------------------|--------|----------------------|
| 1                                                                | Sept, 1968   | June 1969   | 682080<br>Hooe      | 3 m                                         | 0.75 m | S.R.A. M.D.          |
| 2                                                                | Feb. 1969    | June 1969   | 637069<br>Manxey    | 2 m                                         | 0.7 m  | Farmers              |
| 3                                                                | May 1969     | June 1969   | 687062<br>Hooe      | 8 m                                         | 0.85 m | S.R.A. M.D.          |
| 4                                                                | March 1970   | March 1970  | 646058<br>Manxey    | 2.5 m                                       | 0.45 m | Farmers              |
| 5                                                                | March 1970   | April 1970  | 637067<br>Manxey    | 2.5 m                                       | 0.6 m  | Farmers              |
| 6                                                                | Oct. 1970    | Oct. 1970   | 689079<br>Hooe      | 2 m                                         | 0.8 m  | S.R.A.               |
| 7                                                                | Nov. 1970    | April 1971  | 686079<br>Hooe      | 2.5 m                                       | 0.85 m | S.R.A.               |
| 8                                                                | Autumn 1970  | April 1971  | 653065<br>Manxey    | 3.5 m                                       | 1 m    | S.R.A.               |
| 9                                                                | Feb. 1971    | Feb. 1971   | 636036<br>Mountney  | 2.5 m                                       | 0.7 m  | S.R.A.               |
| 10                                                               | Spring 1971  | May 1971    | 627079<br>Down      | 2 m                                         | 0.8 m  | Farmers              |
| Recleared Nov. 1971 & May 1973 as part of<br>main pumping scheme |              |             |                     | 8 m                                         | 1.3 m  | S.R.A. M.D.          |

S.R.A.—Cleared by Sussex River Authority—infrequently (intervals of 5+ yrs)

S.R.A. M.D.—Cleared by Sussex River Authority as part of main drainage scheme (approx. 5 yr intervals)

Farmers—Cleared by farmers at infrequent intervals (possibly 10–15 yrs)

little harm to the environment, gastropods are easily dislodged and most fall into it. Since presumably the error of the net is constant it yields information about the number of species in the different parts of the tarn (or channel) on any one date. Numbers per unit cannot be given accurately by this method.' Macan further describes the net as unexpectedly selective, some animals tending to cling and others to swim when disturbed. For this reason the record of non-gastropod invertebrates cannot be regarded as complete.

As the muddy bank is the only place to which snails can cling if the clearance has been very thorough, it was decided to make the 3 m bank sweep the basic unit of the sampling technique. The net was held as close to the bank as possible and with the upper edge just level with the water surface. If possible, the operation was carried out as one continuous sweep. At first, the evenness of the sides and the lack of vegetation allowed this, but later it was necessary to lift out the net once or twice during the operation to alter its direction. From time to time deeper sweeps, mid-channel sweeps and samples of mud and vegetation were also taken.

Three stations were chosen for regular sampling at each channel. One was about 5 m from the 'end' section, one was the same distance from the junction of an uncleared channel and the third was halfway between the first two stations. As it is difficult to make the vegetation samples comparable quantitatively, results are based on the bank sweeps.



In order to check certain hypotheses related to the geographical position of the channels, a detailed west to east transect was carried out on the 12 August 1973 (Table 7). The grid reference is TQ 6008-6909 and the line of the transect is shown on the map (Fig. 1). In each of the 9 adjacent kilometre squares, 2 adjacent channels at right angles to each other were sampled by the standard 3 × 3 m bank sweeps. In October 1977 collections were made from 6 of the 10 main study channels so extending the knowledge of the colonization pattern up to a period of 8 years. Further sampling was carried out in 26 channels (not recently cleared) from March to August 1978 (a-z on Fig. 1). The results are shown in Table 8.

The gastropods from each collection were identified and in most cases counted. Other macroscopic invertebrates were identified as far as time allowed (Table 9). Vegetation was recorded in the field and from the regular collections (Fig. 4).

The difficulty of sampling on a strictly quantitative basis makes it unwise to apply statistical tests to the numbers of snails in each collection. However, for presence or absence of species or groups of species in a large number of collections, the Chi-squared test has been used to compare the actual data with the theoretically expected figure if distribution had been uniform throughout the Levels.

## RESULTS

a. *Gastropods in main study channels.* Fig. 2 shows the rapid increase in populations during the 2 years following clearance, while the number of species continued to increase during the third and fourth years. The population numbers do not include *Potamopyrgus jenkinsi* which was only found in channels 3 and 9, but occurred in thousands in each sample, other species being much less abundant. At the last sampling, in October 1977, a precise count of individual snails was not made; the mean number of species had declined slightly.

Table 2 shows the species of gastropods recorded each year from regular sampling of the 10 main study channels, arranged in order from west to east. Throughout this account the following grouping of species is used. Group A contains 7 species, each collected from less than half the main study channels; except for *Potamopyrgus jenkinsi* and *Armiger crista* they were more frequent in the west. Group B contains 8 species, each collected from 70–90% of the main study channels; except for *Gyraulus albus* and *Bathyomphalus contortus*, they were more frequent and in some cases more abundant in the west. Group C includes 5 species, each of which was frequent in all the main study channels and abundant in most of them. The rapid colonization and its similar pattern in all channels is apparent. These tendencies are exaggerated by this Table as it includes species that occurred only once a year, as well as those that were present regularly in the monthly samples. The slower colonization of the first few months shows up better in Fig. 2.

The results of one collection from each channel in the second August or September following clearance, are shown in Table 3. The same general pattern is seen as in Table 2, but there are very few records in Group A and over twice as many records for the 5 western channels as for the 5 eastern channels in Group B. Group C species are well established with large populations in some channels, especially in the east. Very small numbers of individuals and species are recorded in channels 3 and 10 where very drastic clearance had taken place and where recent treatment with dalacide was noted.

Out of a total of 20 species, channels in the west show a mean of 14.6 for the 2–4 year period. Those in the east show a mean of 11.1 over the same period. When the single sample (2nd August or September after clearance) is considered, the corresponding means are 7.2 and 6.0. Channels 10, 3 and 6 show certain anomalies which are discussed later. In order to compare the expected and observed numbers of each of the three groups of species a chi-squared test was used. This showed that the total occurrences of Group A and B species are significantly greater in the 5 western channels than in the 5 eastern ones.  $P < .001$ . In other words the probability of these results occurring by chance alone is less than 1 in 1000.



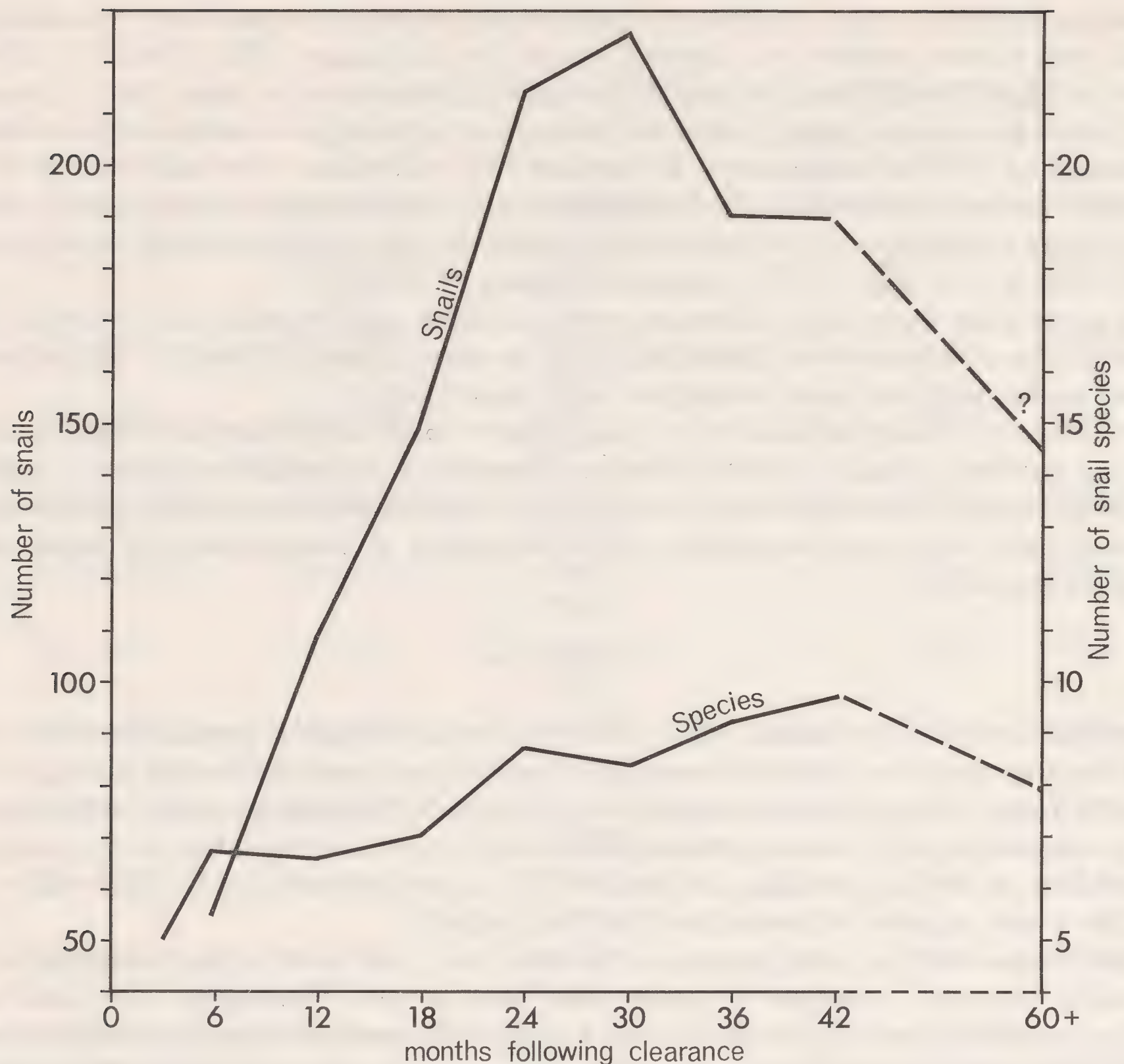


Fig. 2. Mean numbers of individual snails and of snail species recorded (3 by 3 m bank sweeps) following clearance of main study channels.

Fig. 3 combines information on the numbers of species with that of sample size in each channel. September sampling was chosen as this rules out the exceptionally large numbers of young snails in June and July and allows for the stabilization of the population at the end of the summer. In one or two cases August figures were used, where there was no September sampling. In year 2, if the much widened and deepened channels 3 and 10 are omitted and the large population of *Potamopyrgus jenkinsi* in channel 9 is ignored, the rest of the sample figures are very close, being from west to east 195, 144, 161, 157, 168, 252, 259, 198. When these figures are further analysed, it is found that the proportion of Group C snails in each sample is 87%, 90%, 82%, 87%, 85%, 99%, 97%, 98% respectively. The corresponding species numbers are 11, 8, 8, 8, 8, 7, 6, 7.

Table 4 shows the mean number of gastropods of each species in the collections made at 6-monthly periods following clearance. *Potamopyrgus* is omitted as its presence in only two channels in very large numbers would give an unbalanced picture of the general colonization pattern. *Lymnaea peregra* and *Planorbis planorbis* made up 75.2% of all snails collected during the first 6 months and continued to comprise about 50% of the total for the following 18 months. They bred successfully and built up large populations in most channels in the summer following clearance, whether this took place in spring or autumn. From 2½ to 3½ years after clearance these two species made up about 30% of the total number of snails collected. Other Group C



TABLE 2

Gatropod species recorded during each year following clearance in main study channels ( $3 \times 3$  m bank sweeps)

| Five western channels                                |    |    |                |    |    |              |    |    |           | Five eastern channels |    |    |    |    |   |    |  |  |  |
|------------------------------------------------------|----|----|----------------|----|----|--------------|----|----|-----------|-----------------------|----|----|----|----|---|----|--|--|--|
| Down Level                                           |    |    | Mountney Level |    |    | Manxey Level |    |    |           | Hooe Level            |    |    |    |    |   |    |  |  |  |
| Channel                                              | 10 | 9  | 2              | 5  | 8  | 1            | 2  | 3  | 4         | 7                     | 3  | 6  |    |    |   |    |  |  |  |
| Years following clearance                            | 1  | 2  | 1              | 2  | 3  | 4            | 1  | 2  | 3         | 4                     | 1  | 2  | 3  | 4  | 1 | 2  |  |  |  |
| Group A                                              |    |    |                |    |    |              |    |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>Aplexa hypnorum</i>                               | x  |    |                | †  |    | x            |    |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>Anisus vorticulus</i>                             |    |    | x              | x  |    |              |    |    |           |                       |    |    |    |    |   | x  |  |  |  |
| <i>Potamopyrgus jenkinsi</i>                         |    | †* | *              |    |    |              |    |    |           |                       |    |    |    | *  |   |    |  |  |  |
| <i>Lymnaea truncatula</i>                            |    | †  |                |    |    | †            |    |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>Arniger crista</i>                                |    | †  | x              |    |    |              |    |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>Planorbarius corneus</i>                          | x  |    |                | x  |    |              |    |    |           |                       |    |    |    | x  |   |    |  |  |  |
| <i>Segmentina nitida</i>                             | x  |    |                |    | x  |              |    |    |           |                       |    |    |    |    |   | x  |  |  |  |
| Group B                                              |    |    |                |    |    |              |    |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>Hippeutis complanatus</i>                         |    | †  |                | †  | x  | x            |    |    |           |                       |    |    |    |    |   | x  |  |  |  |
| <i>Anisus vortex</i>                                 | x  | †x | x              | †x | *  | x            | *  |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>Valvata macrostoma</i>                            | *  |    | x              | x  | x  | x            | *  |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>Gyraulus albus</i>                                |    |    | *              | x  | x  | *            |    |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>Bathymphalus contortus</i>                        | x  |    | x              | †x | *  | x            | *  |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>Valvata cristata</i>                              | x  | †x | x              | †x | x  | x            | x  |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>Lymnaea palustris</i>                             | x  | †x | x              | †x | x  | x            | x  |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>L. stagnalis</i>                                  | x  | x  | x              | x  | x  | x            | x  |    |           |                       |    |    |    |    |   |    |  |  |  |
| Group C                                              |    |    |                |    |    |              |    |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>Bithynia leachii</i>                              | x  | †x | *              | †* | *  | *            | *  |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>B. tentaculata</i>                                | *  | x  | *              | *  | *  | *            | *  |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>Physa fontinalis</i>                              | x  | x  | x              | †x | x  | *            | *  |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>Planorbis planorbis</i>                           | *  | †* | *              | †x | *  | *            | *  |    |           |                       |    |    |    |    |   |    |  |  |  |
| <i>Lymnaea peregra</i>                               | *  | †* | *              | †x | *  | *            | *  |    |           |                       |    |    |    |    |   |    |  |  |  |
| Total number of species recorded each year           |    |    |                |    |    |              |    |    |           |                       |    |    |    |    |   |    |  |  |  |
|                                                      | 11 | 9  | 9              | 13 | 15 | 14           | 15 | 11 | 12        | 8                     | 10 | 12 | 10 | 10 | 5 | 12 |  |  |  |
| total number of species recorded during study period |    |    |                |    |    |              |    |    |           |                       |    |    |    |    |   |    |  |  |  |
|                                                      | 14 | 12 |                | 16 | 15 | 16           | 10 | 14 | Mean 11.2 |                       |    |    | 10 | 10 |   | 12 |  |  |  |

Key † present in sample before dredging.

x denotes presence of species in at least one monthly collection.

$x$  denotes over 10 individuals in at least one monthly collection.

\* denotes over 25 individuals in at least one monthly collection.



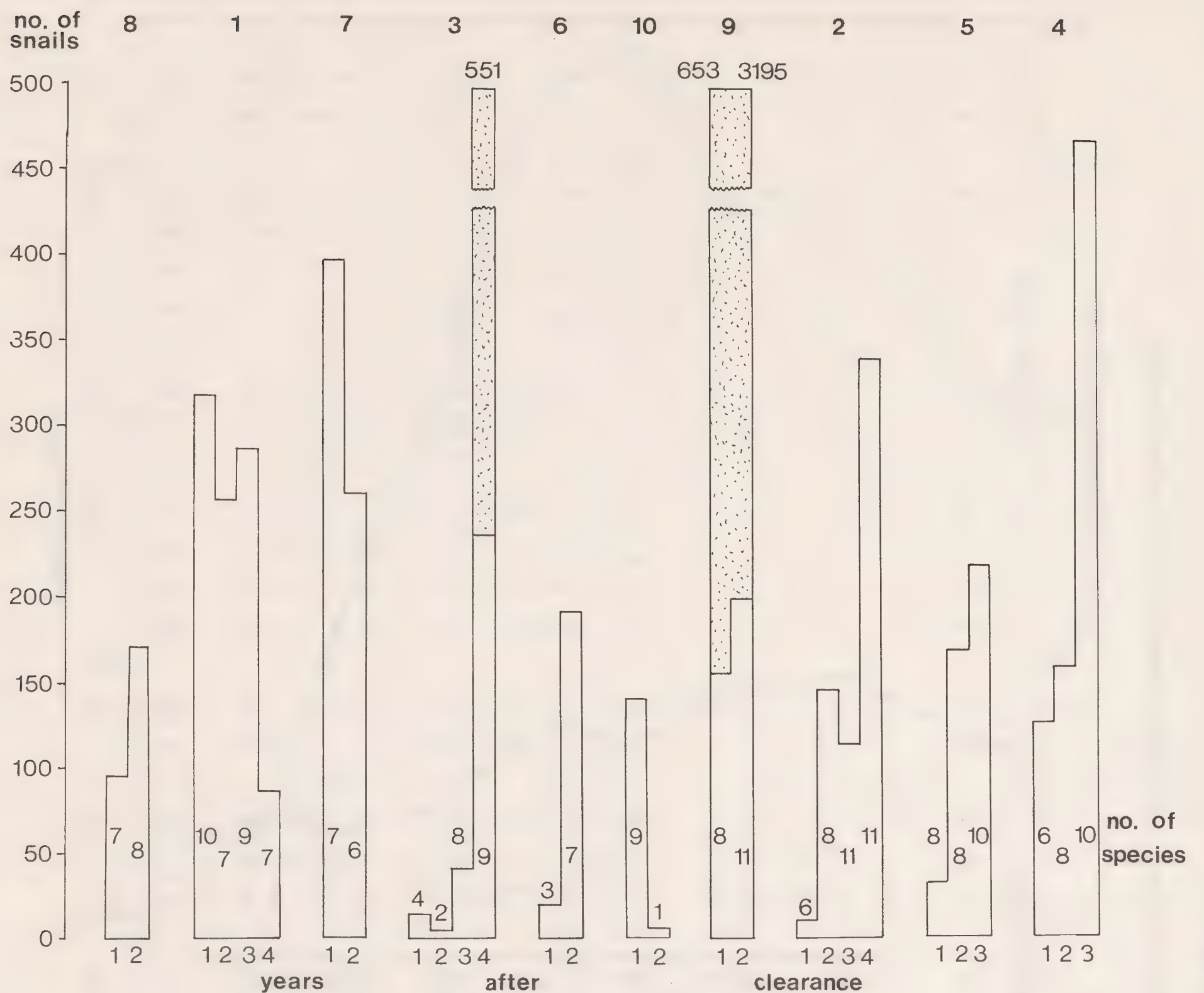


Fig. 3. Numbers of individual snails and of snail species recorded each September (or August) following clearance. Contribution of *Potamopyrgus jenkinsi* to totals in channels 3 and 9 stippled. Channel numbers in bold face at top.

species were also present and bred in the second year in most channels. Group A and B species were usually present in small numbers in the first year, but there were large populations of *Anisus vortex* in channel 8, *Bathyomphalus contortus* in channel 1 and *Potamopyrgus* in channel 9. These 3 species and *Valvata macrostoma* showed large populations in a few channels in the second, third and fourth years.

The tendency was to restore the gastropod community present before clearance in the 4 channels for which data were available, as can be seen from Table 2. This was accomplished within 2 years, but *Hippeutis complanatus*, *Planorbarius corneus* and *Armiger crista* were slower than other species to re-establish themselves. *Lymnaea stagnalis* and *L. palustris* although widely distributed were nowhere abundant.

b. *Gastropods in the rest of the sampling programme.* The results of sampling in 96 channels throughout the Levels in August 1971 are shown in Table 5. A chi-squared test shows that the total number of occurrences of Group C gastropods is significantly greater ( $P < .001$ ) in the northeast of the Levels, (Col. 4) than in the northwest (Col. 1). The total number of occurrences of Group A and B gastropods is significantly greater  $P = 0.01-0.05$  in the northwest than the northeast. *Anisus vortex* occurred a significantly greater number of times in the northwestern channels (Col. 1) than in the northeastern ones (Col. 4) ( $P = 0.01-0.001$ ).



COLONIZATION OF DRAINAGE CHANNELS ON THE PEVENSEY LEVELS (EAST SUSSEX)

TABLE 3

Gastropod species in second August or September following clearance in 10 main study channels  
(3 × 3 m bank sweeps)

|                                                 | Down level | Mountney level | Manxey level |   |   |   | Hooe level East |   |   |   |
|-------------------------------------------------|------------|----------------|--------------|---|---|---|-----------------|---|---|---|
| West Channels                                   | 10         | 9              | 2            | 5 | 4 | 8 | 1               | 7 | 3 | 6 |
| Group A                                         |            |                |              |   |   |   |                 |   |   |   |
| <i>Aplexa hypnorum</i>                          |            |                |              |   |   |   |                 |   |   |   |
| <i>Anisus vorticulus</i>                        |            |                |              |   |   |   |                 |   |   |   |
| <i>Potamopyrgus jenkinsi</i>                    |            | *              |              |   |   |   |                 |   |   |   |
| <i>Lymnaea truncatula</i>                       |            |                |              |   |   |   |                 |   |   |   |
| <i>Armiger crista</i>                           |            | *              |              |   |   |   |                 |   |   |   |
| <i>Planorbarius corneus</i>                     |            |                |              |   |   |   | *               |   |   |   |
| <i>Segmentina nitida</i>                        |            |                |              |   |   |   |                 |   |   |   |
| Group B                                         |            |                |              |   |   |   |                 |   |   |   |
| <i>Hippeutis complanatus</i>                    |            |                |              |   |   |   |                 |   |   |   |
| <i>Anisus vortex</i>                            |            | x              | x            | x | x | x |                 |   |   |   |
| <i>Valvata macrostoma</i>                       |            |                | x            |   | x |   |                 |   | x | x |
| <i>Gyraulus albus</i> ,                         |            |                | x            |   |   |   | x               |   | x |   |
| <i>Bathyomphalus contortus</i>                  |            |                | x            | x | x | x |                 | x |   |   |
| <i>Valvata cristata</i>                         |            | x              |              | x |   |   |                 |   |   |   |
| <i>Lymnaea palustris</i>                        |            | x              |              |   |   | x |                 |   |   |   |
| <i>L. stagnalis</i>                             |            | x              |              |   |   |   |                 |   |   | x |
| Group C                                         |            |                |              |   |   |   |                 |   |   |   |
| <i>Bithynia leachii</i>                         |            | *              | *            | * | x | x | *               | x |   | x |
| <i>B. tentaculata</i>                           |            | *              | *            | * | * | * | *               | x |   | * |
| <i>Physa fontinalis</i>                         |            | x              |              | x | x | x | *               | * |   | * |
| <i>Planorbis planorbis</i>                      |            | x              | x            | x | * | x | *               | * |   | * |
| <i>Lymnaea peregra</i>                          | x          | *              | x            | x | x | x | *               | * |   | * |
| Total no. of spp. recorded<br>from each channel | 1          | 11             | 8            | 8 | 8 | 8 | 7               | 6 | 2 | 7 |

Mean no. of spp. for 5 western channels 7.2, for 5 eastern channels 6.0

Key x—denotes presence of species in collection  
x—denotes over 10 individuals in collection  
\*—denotes over 25 individuals in collection

TABLE 4

Mean number of gastropods per sample for each 6 monthly period following  
clearance in ten study channels (3 × 3 m bank sweeps)

| Six monthly period following clearance              | 1   | 2   | 3   | 4   | 5    | 6   | 7    |
|-----------------------------------------------------|-----|-----|-----|-----|------|-----|------|
| No. of channels included                            | 10  | 10  | 10  | 7   | 7    | 2   | 3    |
| Mean numbers per sample                             |     |     |     |     |      |     |      |
| Groups A and B<br>(less widely distributed species) |     |     |     |     |      |     |      |
| <i>Anisus vortex</i>                                | 0.7 | 4.3 | 5.7 | 5.4 | 12.6 | 1.4 | 22   |
| <i>Bathyomphalus contortus</i>                      | 0.8 | 6.1 | 3.9 | 4.6 | 14.3 | 8.7 | 10.3 |
| <i>Gyraulus albus</i>                               | 2.1 | 0.3 | 2.6 | 2   | 3.6  | 2   | 3.3  |
| <i>Valvata macrostoma</i>                           | 0.3 | 1   | 1.8 | 4.5 | 15.6 | —   | —    |
| Rest of spp. agg. omitting <i>Potamopyrgus</i>      | 1.7 | 1.4 | 3.6 | 2.5 | 7.3  | 4   | 11.5 |



Group C

(species present in all study channels)

|                             |      |       |      |      |      |       |       |
|-----------------------------|------|-------|------|------|------|-------|-------|
| <i>Planorbis planorbis</i>  | 20.6 | 26.3  | 26.8 | 50.8 | 30.7 | 44.1  | 49    |
| <i>Lymnaea peregra</i>      | 17.9 | 28.8  | 41.7 | 70.6 | 51   | 30.1  | 19.3  |
| <i>Bithynia tentaculata</i> | 3.8  | 24.2  | 33.8 | 31.9 | 25.8 | 14    | 42.2  |
| <i>Physa fontinalis</i>     | 1.1  | 9.7   | 18   | 26.5 | 27.7 | 61.7  | 14.4  |
| <i>Bithynia leachii</i>     | 2.2  | 4.8   | 9.5  | 14.5 | 35.4 | 21.1  | 15.9  |
| Total of all spp.           | 51.2 | 106.9 | 147  | 213  | 224  | 187.1 | 187.9 |

TABLE 5

Gastropod species recorded by 1 × 3 m bank sweeps in 96 channels throughout the Levels, Sept. 9 & 10, 1971

|                                                  | 1                            | 2                               | 3                               | 4                   |
|--------------------------------------------------|------------------------------|---------------------------------|---------------------------------|---------------------|
|                                                  | N.W.                         | Centre                          | South                           | N.E.                |
|                                                  | Down & West of Manxey Levels | E. Manxey & West of Hooe Levels | Mountney & Pevensey Bdge Levels | North of Hooe Level |
| Number of channels sampled                       | 24                           | 24                              | 24                              | 24                  |
| Number of channels in which species was recorded |                              |                                 |                                 |                     |
| Group A                                          |                              |                                 |                                 |                     |
| <i>Aplexa hypnorum</i> (Linnaeus)                | 0                            | 0                               | 0                               | 0                   |
| <i>Anisus vorticulus</i> (Troschel)              | 0                            | 4                               | 1                               | 0                   |
| <i>Potamopyrgus jenkinsi</i> (Smith)             | 0                            | 0                               | 5                               | 0                   |
| <i>Lymnaea truncatula</i> (Müller)               | 0                            | 0                               | 0                               | 0                   |
| <i>Armiger crista</i> (Linnaeus)                 | 0                            | 0                               | 0                               | 0                   |
| <i>Planorbarius corneus</i> (Linnaeus)           | 7                            | 0                               | 0                               | 0                   |
| <i>Segmentina nitida</i> (Müller)                | 5                            | 0                               | 2                               | 0                   |
| Group B                                          |                              |                                 |                                 |                     |
| <i>Hippeutis complanatus</i> (Linnaeus)          | 1                            | 0                               | 0                               | 2                   |
| <i>Anisus vortex</i> (Linnaeus)                  | 1                            | 12                              | 4                               | 5                   |
| <i>Valvata macrostoma</i> Mörch                  | 1                            | 3                               | 1                               | 0                   |
| <i>Gyraulus albus</i> (Müller)                   | 0                            | 0                               | 0                               | 2                   |
| <i>Bathyomphalus contortus</i> (Linnaeus)        | 2                            | 4                               | 4                               | 4                   |
| <i>Valvata cristata</i> (Müller)                 | 1                            | 3                               | 1                               | 0                   |
| <i>Lymnaea palustris</i> (Müller)                | 5                            | 1                               | 3                               | 2                   |
| <i>L. stagnalis</i> (Linnaeus)                   | 2                            | 8                               | 1                               | 3                   |
| Group C                                          |                              |                                 |                                 |                     |
| <i>Bithynia leachii</i> (Sheppard)               | 0                            | 6                               | 4                               | 7                   |
| <i>B. tentaculata</i> (Linnaeus)                 | 4                            | 13                              | 13                              | 14                  |
| <i>Physa fontinalis</i> (Linnaeus)               | 6                            | 8                               | 6                               | 13                  |
| <i>Planorbis planorbis</i> (Linnaeus)            | 14                           | 13                              | 12                              | 20                  |
| <i>Lymnaea peregra</i> (Müller)                  | 9                            | 10                              | 13                              | 22                  |

Table 6 shows the results of sampling in 12 adjacent channels on Manxey Level and 8 adjacent channels on Hooe Level. The trend shown in Tables 2 and 3 is even more marked, with a mean of 9.8 species for the western channels (Manxey Level) and 4.8 for the eastern channels (Hooe Level). Further confirmation of the differences between west and east was obtained from the transect, Table 7. One marked feature of these results is that adjacent and often adjoining channels showed a great contrast in the species lists, especially on Down Level. When each pair of channels was considered together, the mean number of species for each Level was in broad agreement with the results of the other sampling programme. Again a chi-squared test shows that the total occurrences of Group A and B gastropods were significantly greater ( $P = 0.01-0.001$ ) in the 3 pairs of western channels than in the 3 pairs of eastern channels.



## COLONIZATION OF DRAINAGE CHANNELS ON THE PEVENSEY LEVELS (EAST SUSSEX)

TABLE 6

Gastropod species recorded in 12 adjacent channels (Manxey) and 8 adjacent channels (Hooe) 3 × 3 m bank sweeps

|                                | March 27 and April 4, 1971.<br>Manxey Level |   |    |    |    |    |     |   |    |   |   |   | Sept. 12, 1971.<br>Hooe Level |   |   |     |   |   |   |   |
|--------------------------------|---------------------------------------------|---|----|----|----|----|-----|---|----|---|---|---|-------------------------------|---|---|-----|---|---|---|---|
|                                | A                                           | B | C  | D  | E  | F  | G   | H | I  | J | K | L | M                             | N | O | P   | Q | R | S | T |
| Group A                        |                                             |   |    |    |    |    |     |   |    |   |   |   |                               |   |   |     |   |   |   |   |
| <i>Aplexa hypnorum</i>         |                                             |   |    |    |    |    |     |   |    |   |   |   |                               |   |   |     |   |   |   |   |
| <i>Anisus vorticulus</i>       |                                             |   |    |    |    |    |     |   |    |   |   |   |                               |   |   |     |   |   |   |   |
| <i>Potamopyrgus jenkinsi</i>   |                                             |   |    |    |    |    |     |   |    |   |   |   |                               |   |   |     |   |   |   |   |
| <i>Lymnaea truncatula</i>      |                                             |   |    |    |    |    |     |   |    |   |   |   |                               |   |   |     |   |   |   |   |
| <i>Armiger crista</i>          |                                             |   |    |    |    |    |     |   |    |   |   |   |                               |   |   |     |   |   |   |   |
| <i>Planorbarius corneus</i>    | x                                           |   |    |    |    |    |     |   | x  | x |   |   |                               |   |   |     |   |   |   |   |
| <i>Segmentina nitida</i>       |                                             |   |    |    | x  | x  | x   |   |    |   |   |   |                               |   |   |     |   |   |   |   |
| Group B                        |                                             |   |    |    |    |    |     |   |    |   |   |   |                               |   |   |     |   |   |   |   |
| <i>Hippeutis complanatus</i>   | x                                           | x |    | x  |    |    |     |   |    |   |   | x |                               |   |   |     |   |   |   |   |
| <i>Anisus vortex</i>           | *                                           | * | *  | *  | x  | *  | x   | x | *  | x | x | x |                               |   |   |     |   |   |   |   |
| <i>Valvata macrostoma</i>      | *                                           | * | x  | x  | x  | x  | *   | x | x  |   |   | x |                               |   |   |     |   |   |   |   |
| <i>Gyraulus albus</i>          |                                             |   |    |    |    |    |     |   |    |   |   |   |                               |   |   |     |   |   |   |   |
| <i>Bathyomphalus contortus</i> | *                                           | x | x  | x  |    | x  | x   | x | x  |   | x | x |                               | * | x |     |   |   |   | x |
| <i>Valvata cristata</i>        | x                                           | x |    |    |    | x  | x   |   | x  |   | x |   |                               |   |   |     |   |   |   |   |
| <i>Lymnaea palustris</i>       |                                             |   | x  | x  | x  | x  | x   | x | x  |   | x |   |                               |   |   |     |   |   |   |   |
| <i>L. stagnalis</i>            | x                                           |   | x  | x  | x  | x  |     |   | x  | x | x | x |                               |   | x | x   |   | x |   | x |
| Group C                        |                                             |   |    |    |    |    |     |   |    |   |   |   |                               |   |   |     |   |   |   |   |
| <i>Bithynia leachii</i>        | x                                           | x | x  | x  | x  | x  | x   | x | x  | x | x | x |                               |   | x | x   |   | x |   | x |
| <i>B. tentaculata</i>          | *                                           | x | x  | x  | x  | x  | x   | x | x  |   | x | x |                               | x | x | x   |   | x | x | x |
| <i>Physa fontinalis</i>        | x                                           |   | x  | x  | x  |    | x   |   | x  |   |   |   |                               | x | x | *   | x |   | x | x |
| <i>Planorbis planorbis</i>     | x                                           | x | x  | *  | x  | x  | x   | x | x  | x | x | x |                               | x | * | *   | x | x | x | x |
| <i>Lymnaea peregra</i>         | x                                           | x | x  | x  | x  | *  | x   | x | x  |   | x | x |                               | x | x | *   | x | x | x | x |
|                                |                                             |   |    |    |    |    |     |   |    |   |   |   |                               |   |   |     |   |   |   |   |
| Total spp. recorded            | 12                                          | 9 | 10 | 11 | 10 | 11 | 11  | 8 | 12 | 5 | 9 | 9 | 5                             | 7 | 6 | 3   | 3 | 5 | 4 | 6 |
| Mean no. spp./channel          |                                             |   |    |    |    |    | 9.8 |   |    |   |   |   |                               |   |   | 4.8 |   |   |   |   |

Between March and August, 1978 an area in the southwest of Hooe Level was surveyed in some detail (channels a–z in Fig. 1) and the results are shown in Table 8. The rarer species *Aplexa hypnorum*, *Anisus vorticulus*, *Segmentina nitida* and *Valvata macrostoma* were present in many of the samples and the last two were abundant. *Valvata piscinalis*, *Anisus leucostoma* and *Acroloxus lacustris* were also found here in very small numbers. In general Group A and B species were much better represented than in the other sampling programmes on Hooe Level.

During the whole 10 years of study, *Anisus vortex* was never recorded east of Waller's Haven and showed large populations only in the centre and west. *Gyraulus albus* was only recorded once or twice from a large central area, including most of Manxey Level. *Potamopyrgus jenkinsi* was almost entirely limited to a few channels near the sea where it occurred in large numbers. There were a few small isolated inland populations. *Segmentina nitida* was not recorded east of Waller's Haven.

c. *Plants and invertebrate (non-gastropod) macroscopic fauna.* Fig. 4 shows the number of invertebrate taxa (other than gastropods), identified and recorded during the two years following clearance in the 10 main study channels. Table 9 shows the species which were identified. Again the difference between channels in the west and east is apparent and this would be even more marked if the 3rd and 4th years had been taken into account. Channel 6 in the east is somewhat anomalous. When the vegetation pattern is taken into account, it may be



TABLE 7

Gastropods recorded in 3 × 3 m bank sweeps in W-E transect August, 1973.

| Channels                          | Down Level |    |    |     |     |      | Manxey Level |    |   |     |    |    | Hooe Level |    |      |     |    |    |
|-----------------------------------|------------|----|----|-----|-----|------|--------------|----|---|-----|----|----|------------|----|------|-----|----|----|
|                                   | I          |    | II |     | III |      | IV           |    | V |     | VI |    | VII        |    | VIII |     | IX |    |
|                                   | 1          | 2  | 3  | 4   | 5   | 6    | 7            | 8  | 9 | 10  | 11 | 12 | 13         | 14 | 15   | 16  | 17 | 18 |
| <b>Group A</b>                    |            |    |    |     |     |      |              |    |   |     |    |    |            |    |      |     |    |    |
| <i>Aplexa hypnorum</i>            |            |    |    |     |     |      |              |    |   |     |    |    |            |    |      |     |    |    |
| <i>Anisus vorticulus</i>          |            | x  |    |     |     | x    |              | x  | x | x   | x  |    |            |    |      |     |    | x  |
| <i>Potamopyrgus jenkinsi</i>      |            |    |    |     |     |      |              |    |   | *   |    |    |            |    |      |     |    |    |
| <i>Lymnaea truncatula</i>         |            |    |    |     |     |      |              |    |   |     |    |    |            |    |      |     |    |    |
| <i>Armiger crista</i>             |            |    | x  |     | x   |      |              |    | x |     |    |    |            |    |      |     |    |    |
| <i>Planorbarius corneus</i>       |            |    |    |     |     | x    |              | x  | x |     |    |    |            |    |      |     |    |    |
| <i>Segmentina nitida</i>          |            | x  |    | x   |     | x    |              |    |   |     |    |    |            |    |      |     |    |    |
| <b>Group B</b>                    |            |    |    |     |     |      |              |    |   |     |    |    |            |    |      |     |    |    |
| <i>Hippeutis complanatus</i>      |            | x  |    | *   | x   | x    | x            |    |   |     |    |    |            |    |      |     |    |    |
| <i>Anisus vortex</i>              |            | x  | x  |     | x   | x    | *            | x  |   |     | x  | x  |            |    |      |     |    |    |
| <i>Valvata macrostoma</i>         |            | x  |    | x   |     |      |              |    |   |     |    |    |            |    |      |     |    | x  |
| <i>Gyraulus albus</i>             |            |    |    |     | x   |      |              | x  |   |     | x  |    |            |    |      |     |    | x  |
| <i>Bathyomphalus contortus</i>    |            | x  | *  |     | x   | x    | *            | x  | x | x   |    |    |            |    | x    | x   |    |    |
| <i>Valvata cristata</i>           |            |    |    |     |     |      | x            |    | x |     |    |    |            |    |      |     |    |    |
| <i>Lymnaea palustris</i>          |            | x  |    |     |     | x    |              |    |   |     | x  |    |            |    |      |     |    |    |
| <i>L. stagnalis</i>               |            |    | x  |     |     | x    |              | x  |   |     |    |    |            |    |      | x   |    |    |
| <b>Group C</b>                    |            |    |    |     |     |      |              |    |   |     |    |    |            |    |      |     |    |    |
| <i>Bithynia leachii</i>           |            | x  | x  |     |     | x    | x            |    |   |     |    |    |            |    |      | x   | x  |    |
| <i>B. tentaculata</i>             |            | x  |    |     |     | *    | x            | x  | x | x   | x  | x  | x          | x  | x    | *   |    | x  |
| <i>Physa fontinalis</i>           |            |    |    |     |     |      | x            | x  |   |     | x  | x  |            |    | x    | x   |    | x  |
| <i>Planorbis planorbis</i>        |            |    | *  | x   |     | *    | x            | x  |   | x   | x  |    | *          | x  | x    | *   | x  | x  |
| <i>Lymnaea peregra</i>            | x          | x  | *  |     |     | x    | x            | x  |   |     | x  | x  | x          | x  | x    | *   | x  | x  |
| No. of spp. recorded              | 1          | 10 | 7  | 4   | 5   | 12   | 9            | 10 | 6 | 5   | 8  | 4  | 3          | 3  | 5    | 7   | 3  | 7  |
|                                   |            | 10 |    | 10  |     | 14   |              | 13 |   | 8   |    | 8  |            | 3  |      | 7   |    | 8  |
| Mean no. of spp./channel          |            |    |    | 6.5 |     |      |              |    | 7 |     |    |    |            |    |      | 4.7 |    |    |
| Mean no. of spp./pair of channels |            |    |    |     |     | 11.3 |              |    |   | 9.7 |    |    |            |    |      | 6   |    |    |

seen that in those channels where *Lemna trisulca* is dominant and there are abundant submerged species, more invertebrate taxa are recorded than where there is a cover of *L. minor* or *L. polyrrhiza* or where no *Lemna* species are present. This trend matches the one for the gastropods, and if all the animals had been identified to species it would have been even more marked. Leeches, flatworms and crustaceans were more evenly distributed than insects, which were more diversified and abundant in the west. A chi-squared test on the 2 species of water louse showed that the occurrence of *Asellus meridianus* was significantly greater ( $P = < .001$ ) than that of *A. aquaticus* in the 5 western channels.

During the rapid survey of 6 out of 10 of the channels in October 1977, the flatworm *Dugesia tigrina* (several individuals) was recorded for the first time. This may be the first record of an introduced American species (Reynoldson, 1967) on the Levels and the intention is to follow up its spread.

Table 10 shows that the water shrimp, *Gammarus pulex*, the flatworms *Polycelis nigra* and *tenuis* agg. *Dugesia lugubris* and *polychroa* agg. and the water louse *Asellus aquaticus* are early colonizers in all channels (except *G. pulex*, strangely absent in 11), becoming established during the first 6 months to one year (except for the 2 flatworms in channel 3). None of the rest of the species was found in all channels. The flatworm, *Dendrocoelum lacteum* was not recorded from the 3 western channels or from channel 3 in the east.



TABLE 8  
Gastropods recorded in adjacent channels in South-West of Hooe Level April-July 1978  
(3 x 3 m bank sweeps) See Map Fig. 1 for location

|                                                                                               | Channels |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |    |    |   |   |    |    |      |
|-----------------------------------------------------------------------------------------------|----------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|---|----|----|---|---|----|----|------|
|                                                                                               | a        | b  | c  | d  | e  | f  | g  | h  | i  | j  | k  | l  | m  | n  | o  | p  | q  | r | s | t  | u  | v | w | x  | y  | z    |
| Group A                                                                                       |          |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |    |    |   |   |    |    |      |
| <i>Aplexa hypnorum</i>                                                                        | x        | x  |    | x  |    |    | x  | x  |    |    |    | x  |    |    |    | x  |    |   |   |    |    |   |   |    |    |      |
| <i>Anisus vorticulus</i>                                                                      |          |    |    |    |    |    |    |    | x  |    |    |    | x  |    | x  | x  |    |   |   |    |    |   |   | x  |    |      |
| <i>Potamopyrgus jenkinsi</i>                                                                  |          |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    | x  |   |   |    |    |   |   |    | x  |      |
| <i>Lymnaea truncatula</i>                                                                     |          |    |    |    |    | x  |    |    |    | x  |    |    |    | x  |    | x  |    |   |   |    |    |   |   |    |    | x    |
| <i>Armiger crista</i>                                                                         | x        | x  | x  |    |    |    |    |    |    |    |    |    |    |    |    | x  |    |   |   |    |    |   |   |    |    |      |
| <i>Planorbarius corneus</i>                                                                   |          |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    | x  |   |   |    |    |   |   | x  |    |      |
| <i>Segmentina nitida</i>                                                                      | x        | x  |    | x  |    | x  | x  |    | x  | x  | x  | x  | x  | x  | x  | x  | x  | x | x | x  | x  |   | x |    |    |      |
| *<br>{<br><i>Valvata piscinalis</i><br><i>Anisus leucostoma</i><br><i>Acroloxus lacustris</i> |          |    |    |    |    |    |    | x  |    |    |    |    |    |    |    | x  | x  |   |   |    |    |   | x |    |    | x    |
|                                                                                               |          |    |    |    |    |    |    |    | x  |    |    |    | x  |    |    |    |    |   |   |    |    |   |   | x  |    |      |
|                                                                                               |          |    |    |    |    |    |    |    |    |    |    |    |    | x  |    |    |    |   |   |    |    |   |   |    |    |      |
| Group B                                                                                       |          |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |    |    |   |   |    |    |      |
| <i>Hippeutis complanatus</i>                                                                  | x        |    | x  | x  |    |    |    |    | x  |    | x  |    |    |    |    | x  |    |   |   |    |    |   |   |    |    |      |
| <i>Anisus vortex</i>                                                                          |          |    |    |    |    | x  |    | x  | x  | x  |    | x  | x  | x  | x  | x  | x  |   |   | x  |    |   |   |    |    |      |
| <i>Valvata macrostoma</i>                                                                     | x        | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x |   | x  |    |   | x |    | x  |      |
| <i>Gyraulus albus</i>                                                                         |          |    |    |    |    |    |    | x  |    |    |    |    |    |    |    |    |    |   |   |    |    |   |   |    |    |      |
| <i>Bathymphalus contortus</i>                                                                 | x        | x  | x  | x  | x  | x  | x  |    | x  | x  | x  |    | x  | x  | x  |    |    |   | x | x  |    |   | x | x  | x  | x    |
| <i>Valvata cristata</i>                                                                       | x        | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  |   | x | x  |    |   | x | x  | x  | x    |
| <i>Lymnaea palustris</i>                                                                      | x        | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x |   |    |    |   |   |    | x  | x    |
| <i>L. stagnalis</i>                                                                           |          |    |    | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  |    | x  | x  | x  |   |   |    |    | x |   | x  |    | x    |
| Group C                                                                                       |          |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |    |    |   |   |    |    |      |
| <i>Bithynia leachii</i>                                                                       | x        | x  | x  | x  | x  | x  |    | x  | x  | x  | x  | x  | x  | x  | x  |    |    |   | x | x  |    |   |   | x  | x  | x    |
| <i>B. tentaculata</i>                                                                         | x        | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x |   | x  |    |   | x | x  | x  | x    |
| <i>Physa fontinalis</i>                                                                       | x        | x  | x  | x  | x  | x  | x  | x  | x  | x  |    |    | x  | x  | x  | x  | x  | x |   | x  |    |   | x | x  | x  | x    |
| <i>Planorbis planorbis</i>                                                                    | x        | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x | x | x  |    |   | x | x  | x  | x    |
| <i>Lymnaea peregra</i>                                                                        | x        | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x  | x | x | x  |    |   | x | x  | x  | x    |
| Total spp. recorded                                                                           | 13       | 12 | 11 | 13 | 10 | 13 | 11 | 13 | 15 | 14 | 11 | 11 | 14 | 13 | 14 | 15 | 13 | 7 | 5 | 10 | 10 | 6 | 9 | 11 | 10 | 10   |
| Mean number of spp. per channel                                                               | a-v      |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |    |    |   |   |    |    | 11.3 |

\* not recorded in rest of sampling programme.



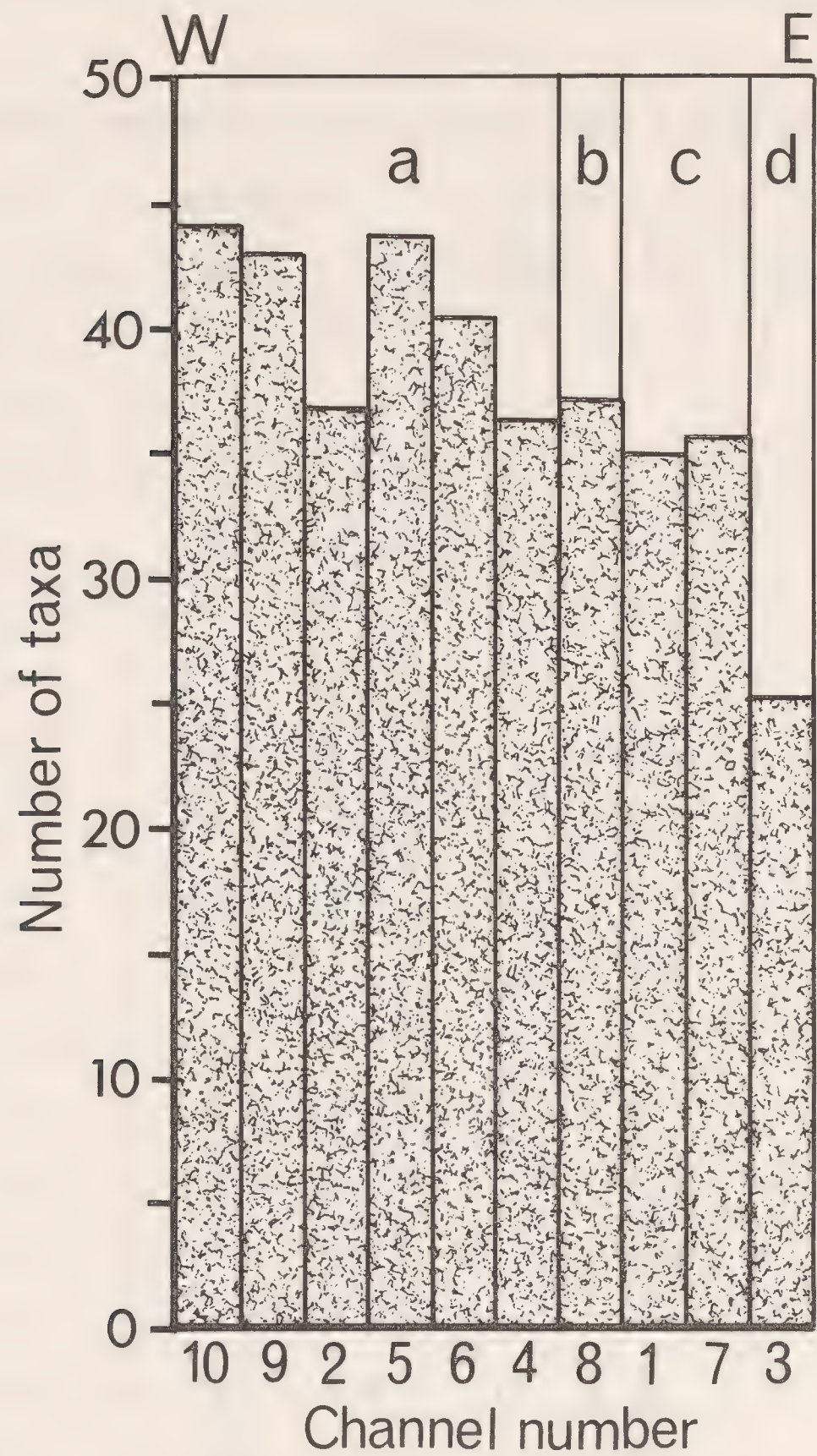


Fig. 4. Vegetation pattern and number of invertebrate taxa (non-gastropod) recorded during two years after clearance of main study channels. a–d Vegetation pattern. a *Lemna trisulca* dominant to other *Lemna* spp. and submerged plants abundant. b *Lemna polyrrhiza* dominant, plus *Azolla filiculoides*. c *Lemna minor* dominant, plus *L. polyrrhiza*, *L. trisulca* and *Woolfia arrhiza*. d Little vegetation, *L. trisulca* absent. NB Channel 6 is not in the correct E-W order.

TABLE 9

Occurrence of non-gastropod invertebrates in 10 study channels  
(only those identified to species included)

|                                                   | W | 10 | 9 | 2 | 5 | 4 | 8 | 1 | 7 | 3 | 6 | E. |
|---------------------------------------------------|---|----|---|---|---|---|---|---|---|---|---|----|
| Platyhelminthes (Turbellaria)                     |   |    |   |   |   |   |   |   |   |   |   |    |
| <i>Polycelis nigra</i> & <i>tenuis</i> agg.       |   | x  | x | x | x | x | x | x | x | x | x |    |
| <i>Dugesia lugubris</i> and <i>polychroa</i> agg. |   | x  | x | x | x | x | x | x | x | x | x |    |
| <i>Dugesia tigrina</i> Girard                     |   | x  |   |   |   |   |   |   |   |   |   |    |
| <i>Dendrocoelum lacteum</i> Müller                |   |    |   |   | x | x | x | x | x |   | x |    |
| Annelida (Hirudinea)                              |   |    |   |   |   |   |   |   |   |   |   |    |
| <i>Glossiphonia heteroclita</i> Linnaeus          |   | x  | x | x | x | x | x | x | x |   | x |    |
| <i>G. complanata</i> (Linnaeus)                   |   | x  | x |   | x | x | x | x | x |   | x |    |
| <i>Erpobdella octoculata</i> (Linnaeus)           |   | x  | x | x | x | x | x | x | x |   | x |    |



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|                                        |   |   |   |   |   |   |   |   |   |   |
|----------------------------------------|---|---|---|---|---|---|---|---|---|---|
| <i>Haemopsis sanguisuga</i> (Linnaeus) | x |   | x | x | x |   | x | x |   | x |
| <i>Theromyzon tessulatum</i> (Müller)  | x |   | x | x | x | x | x | x |   | x |
| <i>Helobdella stagnalis</i> (Linnaeus) |   | x | x |   | x | x | x |   | x | x |
| <i>Hemiclepsis marginata</i> (Müller)  |   |   |   | x |   |   | x |   |   |   |
| Arthropoda (Crustacea)                 |   |   |   |   |   |   |   |   |   |   |
| <i>Gammarus pulex</i> (Linnaeus)       |   | x | x | x | x | x | x | x | x | x |
| <i>G. zaddachi</i> Sexton              |   |   |   |   |   |   |   |   | x |   |
| <i>Asellus aquaticus</i> (Linnaeus)    | x | x | x | x | x | x | x | x | ? | x |
| <i>A. meridianus</i> Rac.              | x | x | x | x | x | x | x | x | ? | x |
| (Arachnida)                            |   |   |   |   |   |   |   |   |   |   |
| <i>Argyroneta aquatica</i> (Linnaeus)  | x | x | x | x | x | x | x | x |   | x |
| (Insecta)                              |   |   |   |   |   |   |   |   |   |   |
| <i>Cloeon dipterum</i> (Linnaeus)      | x | x | x | x | x | x | x | x |   | x |
| <i>Caenis horaria</i> (Linnaeus)       | x | x | x | x | x | x |   |   | x | x |
| <i>Ilyocoris cimicoides</i> (Linnaeus) | x | x | x | x | x | x | x |   |   | x |
| <i>Plea leachi</i> MacGregor           | x | x | x | x | x | x | x | x | x | x |
| <i>Hydrometra stagnorum</i> (Linnaeus) | x | x |   | x | x |   |   |   |   |   |
| <i>Nepa cinerea</i> (Linnaeus)         |   | x | x |   |   |   |   |   |   |   |
| <i>Ranatra linearis</i> (Linnaeus)     |   | x | x |   |   |   |   |   | x |   |

Key x denotes presence in sampling programme.  
x denotes presence in over 30% of samples.

TABLE 10

Number of months after clearance for some common non-gastropod species to occur in samples from ten study channels

|                                                      | West |    |    |   |    |    |    |    |    | East |
|------------------------------------------------------|------|----|----|---|----|----|----|----|----|------|
|                                                      | 10   | 9  | 2  | 5 | 4  | 8  | 1  | 7  | 3  | 6    |
| No. of months after clearance of 1st sampling        | 5    | 1  | 1  | 3 | 2  | 6  | 9  | 8  | 1  | 6    |
| <i>Polycelis nigra</i> & <i>P. teunis</i> agg.       | 7    | 1  | 3  | 3 | 2  | 6  | 9  | 9  | 17 | 6    |
| <i>Gammarus pulex</i>                                | —    | 1  | 6  | 6 | 2  | 6  | 9  | 8  | 2  | 6    |
| <i>Dugesia lugubris</i> and <i>D. polychroa</i> agg. | 8    | 2  | 6  | 7 | 3  | 6  | 9  | 11 | 17 | 9    |
| <i>Asellus aquaticus</i>                             | —    | 11 | —  | — | —  | 10 | 9  | 11 | —  | 6    |
| <i>A. meridianus</i>                                 | —    | 24 | —  | — | —  | 21 | —  | 10 | —  | 14   |
| <i>Asellus</i> spp. agg.                             | 5    | —  | 3  | 9 | 6  | —  | —  | —  | 5  | —    |
| <i>Cloeon dipterum</i> nymphs                        | 8    | 11 | 3  | 9 | 4  | 12 | 11 | 12 | —  | 14   |
| <i>Caenis horaria</i> nymphs                         | 8    | 4  | 3  | 8 | 4  | 12 | —  | —  | 4  | 14   |
| <i>Glossiphonia heteroclita</i>                      | 5    | 17 | 18 | 8 | 12 | 10 | 9  | 15 | —  | 11   |
| <i>Erpobdella octoculata</i>                         | 9    | 7  | 18 | 4 | 6  | —  | 10 | 11 | —  | 7    |
| <i>Haemopsis sanguisuga</i>                          | 11   | —  | 7  | 7 | 6  | —  | 11 | 12 | —  | 16   |
| <i>Dendrocoelum lacteum</i>                          | —    | —  | —  | 8 | 15 | 10 | 14 | 12 | —  | 12   |
| <i>Helobdella stagnalis</i>                          | —    | 16 | 19 | — | —  | —  | 12 | —  | 14 | 22   |

DISCUSSION

The rapid colonization of the drainage ditches after clearance shows that most species are well adapted to the regime. Amongst the gastropods, the 5 species in Group C (see Tables 2 and 3) are the most widespread, the most abundant and always amongst the first colonizers. Further investigation is needed to find out whether the reason for their success is their more rapid movement into newly dredged ditches, higher reproductive capacity, higher survival rate



amongst the young, less demanding environmental needs, including food, or lack of competition from other species. It is probable that all these factors and others play a part, but it would be difficult to prove in the field or the laboratory.

*Lymnaea peregra* is well known to be an undemanding species. Hunter, (1961) in his study on Loch Lomond, stresses the variation in respiratory and feeding behaviour, food requirements and breeding patterns which gives this species a far wider range of habitats than any other freshwater gastropod. In the Pevensey study eggs of this species were found on 18 species of plants, two generations of snails per year were found in channels 5, 6 and 7 and the mean shell length in the breeding season was 11.5 mm from recently cleared channels and 9.4 mm from channels which had been cleared longer ago.

One factor relating to the success of *Planorbis planorbis* on the Levels is probably its ability to resist desiccation (Klekowski, 1959). Some of the channels are virtually dry when dredging operations are carried out especially if they are dredged in early spring when the sluice gates are open and the water level is low in all the ditches. The dredged material is banked up on the sides and contains many empty shells, but also some living ones that may find their way back into the refilled channel after a period of time.

Group A species appear to be the most specialized in their requirements, the only one of the group occurring in any numbers was *Potamopyrgus jenkinsi* and this was limited to channels 3 and 9, nearest to the sea. This species probably illustrates best that environmental conditions rather than accidents of arrival account for the differences between the gastropod fauna of the various channels and Levels. In Britain this species was known only from brackish water until the first inland record in 1893, Macan (1969), since when it has colonized the whole country, Frömming (1956). It is strange that it has not been found throughout the Levels, as being parthenogenetic, it only needs one individual carried by flood or on a bird's foot to found a new colony. Many of the channels are interconnecting, flooding is frequent and was more widespread before the modern improvements in drainage. Opportunities for transport by man and animals from one part of the Levels to another are considerable. If environmental conditions were uniform throughout, all 20 species of gastropods would be much more evenly distributed.

The decrease in the % of the pioneer species *Lymnaea peregra* and *Planorbis planorbis* from 75% to 30% of the total collection over 3½ years and of Group C species as a whole from 89% to 75%, indicates that some kind of succession is operating. It never advances very far in those channels which are cleared at approximately 5 yearly intervals.

The results of combining data on individual snail numbers with those on species numbers show little pattern in the first year, the gastropod populations having hardly recovered from the upheavals of clearance. In year 2, the difference between the means of samples from Manxey Level, channels 2, 4, 5 and 8 and Hooe Level, 1, 6 and 7, is very highly significant ( $P < .001$ ), as far as numbers of individual snails are concerned. The proportion of Group C snails on the three Hooe Level channels is also very highly significantly greater than on Manxey Level. It will be noted that where total sample size is large, Group C is better represented and species number is smaller. Some competition is indicated but more evidence and experiments are needed to elucidate its nature.

The uneven distribution of species is borne out by the wider sampling programme which underlines the contrast between the various Levels and Channels. The conditions in the north and east of Hooe Level, especially east of Waller's Haven, are less favourable for Group A and B species, while Group C species thrive better than in the west.

Table 11 compares the % frequency of occurrence of gastropod species in 5 groups of channels bringing out the differences between both the recently cleared and non-recently cleared channels from different regions of the Levels. The same trend is apparent whether extensive sampling throughout 2–4 years is considered as in columns 1 and 2 or whether the standard single sample ( $3 \times 3$  m bank sweep) is taken as in the other columns. Group A species (the rarer ones) do better in non-recently cleared channels than in recently cleared channels



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TABLE 11

% frequency of occurrence of gastropod species in recently cleared and non-recently cleared channels in the west, centre and east of the Levels

|                                 | recently cleared                                             |        |                          |       | non-recently cleared            |        |       |
|---------------------------------|--------------------------------------------------------------|--------|--------------------------|-------|---------------------------------|--------|-------|
|                                 | all samples<br>as Table 2                                    |        | one sample<br>as Table 3 |       | Transect Aug 1973<br>as Table 6 |        |       |
|                                 | % of channels in which species was found in<br>3 × 3 m sweep |        |                          |       |                                 |        |       |
|                                 | west                                                         | east   | west                     | east  | west                            | centre | east  |
| Group A                         |                                                              |        |                          |       |                                 |        |       |
| <i>Aplexa hypnorum</i>          | 40                                                           | —      | —                        | —     | —                               | —      | —     |
| <i>Anisus vorticulus</i>        | 20                                                           | 20     | 20                       | —     | 33                              | 66     | 17    |
| <i>Potamopyrgus jenkinsi</i>    | 20                                                           | 20     | 20                       | 20    | —                               | 17     | —     |
| <i>Lymnaea truncatula</i>       | 20                                                           | 40     | —                        | —     | —                               | —      | —     |
| <i>Armiger crista</i>           | 40                                                           | 40     | 20                       | —     | 33                              | 17     | —     |
| <i>Planorbarius corneus</i>     | 40                                                           | 20     | —                        | 20    | 17                              | 33     | —     |
| <i>Segmentina nitida</i>        | 80                                                           | —      | —                        | —     | 50                              | —      | —     |
| Mean % Group A spp. per channel | 34.3                                                         | 20     | 8.6                      | 5.7   | 19                              | 19     | 2.4   |
| Group B                         |                                                              |        |                          |       |                                 |        |       |
| <i>Hippeutis complanatus</i>    | 80                                                           | 60     | 40                       | —     | 66                              | 17     | —     |
| <i>Anisus vortex</i>            | 100                                                          | 20     | 100                      | 20    | 66                              | 66     | —     |
| <i>Valvata macrostoma</i>       | 80                                                           | 60     | 60                       | 40    | 33                              | —      | 17    |
| <i>Gyraulus albus</i>           | 60                                                           | 80     | 20                       | 20    | 17                              | 33     | 17    |
| <i>Bathyomphalus contortus</i>  | 80                                                           | 80     | 80                       | 40    | 66                              | 33     | 33    |
| <i>Valvata cristata</i>         | 100                                                          | 40     | 80                       | —     | —                               | 33     | —     |
| <i>Lymnaea palustris</i>        | 100                                                          | 80     | 20                       | 20    | 33                              | 17     | —     |
| <i>L. stagnalis</i>             | 100                                                          | 80     | 60                       | 40    | 33                              | 17     | 17    |
| Mean % Group B spp. per channel | 87.5                                                         | 62.5   | 57.5                     | 22.5  | 39.3                            | 31.1   | 6.4   |
| Group C                         |                                                              |        |                          |       |                                 |        |       |
| <i>Bithynia leachii</i>         | 100                                                          | 100    | 100                      | 100   | 50                              | —      | 33    |
| <i>B. tentaculata</i>           | 100                                                          | 100    | 100                      | 100   | 33                              | 100    | 82    |
| <i>Physa fontinalis</i>         | 100                                                          | 100    | 100                      | 100   | 33                              | 33     | 50    |
| <i>Planorbis planorbis</i>      | 100                                                          | 100    | 100                      | 100   | 50                              | 66     | 100   |
| <i>Lymnaea peregra</i>          | 100                                                          | 100    | 100                      | 100   | 66                              | 66     | 100   |
| Mean % Group C spp. per channel | 100                                                          | 100    | 100                      | 100   | 47.6                            | 53     | 73    |
| Number of channels sampled      |                                                              |        |                          |       |                                 |        |       |
| × no. of times                  | 5 × 15                                                       | 5 × 15 | 5 × 1                    | 5 × 1 | 6 × 1                           | 6 × 1  | 6 × 1 |
| No. spp. recorded               | 20                                                           | 18     | 16                       | 13    | 16                              | 15     | 10    |

(comparing columns 3, 4, 5, 6 and 7 which are single samples). They also did better in the west and centre than in the east (comparing columns 1, 3, 5 and 6 with 2, 4 and 7). Group C species did better in the cleared than the uncleared channels (comparing columns 3–7). Group B did better in the west and centre than in the east (comparing columns 1, 3, 5 and 6 with 2, 4 and 7). Group C on the other hand did better in the east than the west and centre.

The results of the 1978 sampling in the southwest of Hooe Level (Table 8) suggest that areas with a richer snail fauna may be found further east than the other studies had revealed. This area had not been subject to any extensive dredging operation and had remained relatively undisturbed during the 1968–78 period.

Improved pumping schemes and treatment with herbicide have been longer established and more extensive in the east, the vegetation pattern is different and some other invertebrates also occur less frequently. Where a varied vegetation, including *Lemna trisulca* and several submerged species of plants become established, there are more niches for a diversified fauna.



Air breathing insects and gastropods can reach the surface more easily than if it is completely carpeted by *Lemna minor*, *L. polyrrhiza*, *L. gibba* and *Woolfia arrhiza*. The insects are far more easily disseminated than the snails and yet their distribution shows a similar trend to the gastropods, underlining once more the relative importance of environmental conditions compared with 'accidents of arrival'. The appearance of *Dugesia tigrina* in samples from channel 10 in 1977 must have been an 'accident of arrival'. Its follow up should prove interesting.

While the dredging of the channels maintains drainage and rejuvenates the plant and animal community, the extension of pumping schemes, the use of herbicides and the frequent disturbance of the environment will result in the further restriction in distribution or disappearance of some of the rarer species of plants and animals. It is hoped that the proposed Nature Reserve will be sited relevantly and will help to reverse this trend.

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# SEGREGATES OF THE *ARION HORTENSIS* COMPLEX (PULMONATA: ARIONIDAE), WITH THE DESCRIPTION OF A NEW SPECIES, *ARION OWENII*

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(Read before the Society, 19 May 1979)

*Abstract:* The name *Arion hortensis* has been used for three different British species of slug, called **A**, **R** and **B** by Davies (1977). *Arion (Kobeltia) hortensis* Férussac s. s. is defined as having the anatomy and spermatophore of form **R**. *A. (K.) distinctus* Mabille is identified as form **A**, and is thus given an anatomical definition. External features are discussed with reference to original descriptions and identification. Form **B** becomes *A. (K.) owenii* sp. nov.

The subgenus *Kobeltia* is distinguished from the rest of *Arion* by the short spermatophore, which, instead of entering a longer spermatheca duct, is at first held in the atrium by means of a collar attached at or within the entrance to a very short spermatheca duct. Details of the spermatophore, and the structures associated with its attachment, may be used to define the three species hitherto known as the *A. hortensis* complex. *A. intermedius* Normand, although its spermatophore is not known, may also be placed in *Kobeltia* because of its general similarity, and in particular, the very short spermatheca duct and the termination of the epiphallus. The oviduct, which is short and undifferentiated in *A. intermedius*, is long and developed for protrusion in coitus in the other species, in different proportions, and with two alternative forms in one species.

The following account attaches names to the three species already described and figured (Davies, 1977), adding some further observations on external features and identification.

## *Arion (Kobeltia) hortensis* Férussac

1819 *Arion hortensis* Férussac: 65, pl. 2, figs. 4, 5.

1866 ?*Arion anthracius* Bourguignat: 178.

1870 ?*Arion pelophilus* Mabille: 117.

1894 *Arion elongatus* Collinge: 66.

1977 *Arion hortensis* Férussac **R**, Davies: 184.

Férussac's species must be redefined by the form of spermatophore and associated structures. Altena examined Férussac's type, preserved in the Paris Museum, in 1976, and found that it belonged to form **R** (Davies, 1977, p. 187). Of course there was no spermatophore, and the specimen was not quite mature, but the markings suggest **R**, and the oviduct and epiphallus are well enough developed to compare with fresh immature **R**, which can be distinguished from form **A** at a similar stage.



*Diagnostic features of A. hortensis s. s. are:*

- 1) spermatophore short and relatively stout, with a serrated longitudinal ridge; with a hard attachment collar (Davies, 1977, Figs. 2d-f).
- 2) a distinctive structure prominent in the atrium, between the termination of the epiphallus and the spermatheca duct (Davies, 1977, Figs. 4c-d).
- 3) oviduct with a long narrow proximal portion, gradually enlarging into a firm portion which is not greatly exaggerated but is usually smaller than the epiphallus, and a long distal region which is eversible as a slender process during coitus (Davies, 1977, Figs. 5c, 6b). Although the specific differences in the proportions of the oviduct are relative rather than absolute, they are sufficient to allow immediate recognition of the species in normal circumstances.

The external appearance may strongly resemble *A. distinctus* as defined below, but the typical form of *A. hortensis s. s.* is quite easily recognized by

- 1) a reddish tinge in the black or grey head and tentacles.
- 2) a narrower space between the mantle bands, which are parallel or divergent, but not strongly convergent, anteriorly.
- 3) the strong pigmentation described by Férussac, a nearly black dorsum, and blue-black lateral bands bordered by grey, the lowest row of tubercles often strikingly white.

*External variation.* The pigments vary in quantity, but the typical markings are prevalent, at least in Britain. The sole is variable, and changeable, from pale yellow to deep orange. There is usually some yellowing, at or after maturity, especially above the lateral bands, of the tiny white dots which, with the black pigment, produce the blue-grey colour typical of juveniles and some adults. Some individuals are more uniformly yellow-grey, with a wide space between the mantle bands, the bands only slightly heavier and more parallel than in similarly coloured *A. distinctus*. Replacement of some or all of the black pigment by a red, without affecting its distribution, produces a minority of reddish brown or purple slugs in some populations. Darkened, senile animals probably account for *Arion pelophilus* Mabille, which was found in April, a time when these may abound. *A. anthracius* Bourguignat is another dark form, insufficiently described and therefore a doubtful synonym.

*Mating.* Coitus lasts at least 80 minutes, and is a lengthier process than in the other two species.

*Season.* Breeding is mainly in autumn and winter, through until about April.

*Distribution.* In England and Wales and parts of France, *A. hortensis s. s.* usually alternates seasonally with *A. distinctus*. It was recognized by Altena in the Netherlands, but needs confirmation in other countries. Although it is not confined to gardens, it sometimes appears to be more closely associated with them than is *A. distinctus*.

#### *Arion (Kobeltia) distinctus* Mabille

1819 ?*Arion hortensis* var  $\alpha$  Férussac: pl. 2, fig. 6.

1855 *Arion fuscus* (Müller) var *fasciatus* Moquin-Tandon: 2, 14, non *Arion fasciatus* (Nilsson, 1822).

1868 *Arion distinctus* Mabille: 137.

1870 *Arion distinctus* Mabille: 119.

1889 *Arion cottianus* Pollonera: 634, pl. ix, figs. 23, 24.

1897 *Arion coeruleus* Collinge: 444.

1977 *Arion hortensis* Férussac species A Davies: 184.

The type locality of *Arion distinctus* is Sèvres, near Paris. No original material survives. The conclusion that Mabille's name belongs to this species (i.e. form A), and cannot be a synonym of



*A. hortensis* s. s., is supported by repeated experience in the field, in all parts of Britain. Mixed collections of live individuals can generally, in fact, be separated according to the original descriptions of *A. hortensis* and *A. distinctus*, both made from living material; dissection proving them to be form **R** and form **A**, respectively. Mabille's species, which was based on external features only, can therefore be redescribed and extended to coincide with form **A**, even if when so extended, it may not always be distinguishable externally from *A. hortensis* s. s. Externally, confusion is caused by certain colour variations of the two species, and by senile forms, but the anatomy is distinct.

Pollonera (1887, 1889) described typical *A. hortensis* from France, agreeing with Férussac's original description, and with the gross anatomy of form **R**, but also with colour variations which unfortunately led him to include in his *A. hortensis* s. s. both *A. distinctus* Mabille and var. *fasciatus* Moquin-Tandon, which he separated from *Arion fasciatus* (Nilsson). That Moquin-Tandon's var. *fasciatus*, the main form of his composite species, really belongs to form **A** (= *A. distinctus*) is indicated by the account of the eggs—50 to 70 in number,  $2.5 \times 2$  mm, whitish, laid from May to September. This also appears to be the most widespread form in France today. Although Pollonera recognized *A. hortensis* (= form **R**) as a widespread and variable species, he did not recognize form **A** as a second species at least as widespread and as variable. Instead, he named several forms from rather scanty and local material, such as *A. cottianus* from Bardonecchia in the Cottian Alps. His careful anatomical descriptions and drawings hardly lessen the confusion of forms, because all parts appear as fixed, and the firm portion of the oviduct is not distinguished from the soft part which, like the atrium, may be distorted, distended, elongated or telescoped.

*Diagnostic features of A. distinctus are:*

- 1) spermatophore longer, and relatively narrower, than in *A. hortensis* s. s., virtually smooth, or with a very slight longitudinal ridge and denticulations (Davies, 1977, Figs. 2a–c).
- 2) a curved plate over the termination of the epiphallus, quite different in shape and position from the prominent structure in *A. hortensis* s. s. (Davies, 1977, Figs. 4a–b).
- 3) oviduct basically similar to *A. hortensis* s. s., but immediately distinguished by the larger size of the firm portion; either with or without a very large eversible distal portion (Davies, 1977, Figs. 5a–b).

External features noted by Mabille which distinguish typical *A. distinctus* from typical *A. hortensis* s. s. are

- 1) blue-black or cold grey head and tentacles.
- 2) mantle bands rather low, enclosing a wide space, converging at either end, and sometimes even meeting anteriorly, thus almost encircling the mantle.
- 3) general colour yellowish grey.

Other characteristic features fairly commonly seen are

- 1) a break or a steep dip in the right mantle band over the respiratory orifice.
- 2) a fine yellow streak in the mid-dorsal line, at the posterior end, where the sprinkling of yellow dots is particularly heavy.

Mabille gave the absence of lineolation of the foot fringe as another distinction from *A. hortensis*, and this could appear to be so when the samples are of different age-groups. Both species sometimes develop more or less distinct dark transverse lines on the foot fringe, usually at a rather late stage of maturity.

The absolute reliability of any of these external distinctions is extremely doubtful, but they may be very useful, and quite reliable in limited populations.

*External variation.* The pigments vary in quantity, as in *A. hortensis* s. s., and the sole shows the



same range of colour. The light pigments of the body are white in juveniles, and may remain white, especially in the lowest row of tubercles, instead of becoming yellow. The yellowest form, here regarded as the type-form, has rather narrow bands, but in forms with a greater development of dark pigment, and heavier bands, the general appearance approaches that of *A. hortensis* s. s.

*Mating.* Coitus lasts for not more than 30 minutes.

*Season.* Adults appear from rather later in the autumn than *A. hortensis* s. s. and breeding takes place mainly in spring and summer, but may continue throughout the year. The English name 'April slug' recorded by Gray (1857, p. 71), is an apt one for this species.

*Distribution.* *A. distinctus* has been more widely collected than *A. hortensis* s. s., even where both abound, because it is often found alone in summer, but it probably has a wider distribution as well. It has been recognized in much of Europe, and in North America. A set of 15 representative samples (80 specimens) from Sweden, loaned by the Swedish Museum of Natural History, Stockholm, were found to be all this species, with no *A. hortensis* s. s.

### **Arion (Kobeltia) owenii** sp. nov.

1905 ? *Arion hortensis* Férussac var *subfusca* Taylor: 217.

1977 *Arion hortensis* Férussac species **B** Davies: 185.

The history of this rather strikingly well-marked species is surprisingly obscure. It is likely, but unproven, to be at least part of Taylor's var. *subfusca*, which he claimed as a distinct large brown variety of *A. hortensis*, but he does not distinguish it satisfactorily. Large brownish forms of *A. hortensis* s. s., and of *A. distinctus*, also appear, usually rather late in their season, when *A. owenii*, being out of season, is not available for direct comparison. Taylor followed Moquin-Tandon in making *Limax subfuscus* C. Pfeiffer a variety of *A. hortensis*, not *A. subfuscus* (Drap.), but Pfeiffer's description (1821, p. 20) excludes neither possibility. No specimens of *A. owenii* having come to light on the continent, it is regarded as a new species from Ireland and Britain.

The name is taken from the unknown Owen whose name is preserved in the territorial names of Inishowen and Tyrone, in Ireland. The type locality is Buncrana, the capital of Inishowen, East Donegal (Irish Grid ref. C 3432), where the slug was first found by the author, in abundance, in August/September 1968.

The holotype (British Museum Natural History 197910) is a specimen killed on 24 November 1969, selected from the brood of an animal brought from Buncrana in the previous year, opened to show the general features of the anatomy, including a characteristic bulge of the atrium which indicates the position and form of the distinctive lobed structure within. Although fully mature, the animal is not spent: the ovotestis is still fairly large, and lightly pigmented. Paratypes (BMNH 197911/1-6) include slugs killed immediately after mating, with the spermatophore in the atrium, or, later, with the spermatophore in the spermatheca sac. Spermatophores become hard and yellow in alcohol, so they have usually been cleaned and kept in an aqueous solution of borax, where they remain colourless and transparent.

*Diagnostic features of A. owenii* are:

- 1) spermatophore as in *A. hortensis* s. s. and *A. distinctus*, and of intermediate size, but with a strongly spiral serrated ridge; with a hard attachment collar (Davies, 1977, Figs. 2g-h).
- 2) a lobed structure in the atrium, originating near the termination of the epiphallus (Davies, 1977, Figs. 4e-f, 5d).



3) oviduct with a long narrow proximal portion, and a well developed firm portion as in *A. distinctus*; always with eversion to a limited extent during coitus (Davies, 1977, Figs. 5d, 6c).

The external features of *A. owenii* nearly always permit instant recognition. In life, the surface often presents a distinctive appearance, with very regular and rather sharply ridged tubercles. The typical form is a rich brown, with dark bands, with greyish sides and a very pale yellow sole. The general colour may suggest *A. subfuscus*, and the pattern some form of *A. hortensis*, but there is a brown background colour which remains in alcohol, and specimens do not become blue-grey even after years. The mantle bands are parallel, not convergent, at the anterior end. The dark markings are usually somewhat speckled, and may be blotchy or broken. The tentacles are pinkish brown. The foot fringe is clearly lineolated.

*External variation.* As in the other species, the sole may become a richer yellow, or orange. The dark pigment may be very heavy, or much reduced. Some Cornish slugs look rather like a large yellow *A. intermedius*, with only a few dark dots instead of bands. The foot fringe may have dark specks, or no dark pigment. A line of white may or may not be present in the lowest row of tubercles next to the foot fringe.

*Mating.* No observations have been made in the field, but numerous matings in captivity of slugs from Ireland, Cornwall, Wales and England show a uniform pattern. Coitus lasts about 45 minutes, always longer than any time recorded for *A. distinctus*, and less than any time recorded for *A. hortensis s. s.*

*Season.* *A. owenii* matures in the autumn, mostly rather earlier than *A. hortensis s. s.*, and breeds mainly in the winter months.

*Distribution.* *A. owenii* is found in many places in the north of Ireland, and more locally in southern Scotland, Wales, Cornwall and England. Altogether some hundreds of specimens have been examined, but not thousands as in the other species.

#### ACKNOWLEDGEMENTS

A wide-ranging and leisurely scrutiny of the literature was made possible, and also enjoyable, thanks to the helpfulness of staff at the British Museum (Natural History).

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## REVIEW

*A field guide to the land snails of Britain and North-west Europe*. By M. P. Kerney and R. A. D. Cameron, illustrated by Gordon Riley. 288 pp., 24 colour plates, text-illustrated, 392 distribution maps. 8° Collins, 1979. Price £5.50.

This book is the latest in the well-known Collins Field Guide series and is excellent value for money. It is a must for any member interested in British or European non-marine molluscs. The guide starts with introductory sections on general biology of snails, hints on collecting, names and classification, identification, dissection, etc. and even includes a two page glossary of shell terms. The introductory section, mainly by R. A. D. Cameron, ends with a systematic check list.

The main part of the guide consists of systematic descriptions of nearly 300 species, including 10 common greenhouse aliens, this part mainly by our non-marine recorder, Dr. Kerney who is also responsible for the final section of distribution maps. The systematic descriptions are clear, well laid out and illustrated by Gordon Riley's excellent colour and black and white drawings. These are among the best illustrations of snails that I have ever seen, although I must confess that having seen the originals, the drawings of *Acicula* species have lost a little in the printing process. A very useful feature of the drawings is that related species are all illustrated at the same magnification which greatly facilitates identification. The general characters of each family are described before detailed specific descriptions. This section ends with a bibliography and an index to the species.

The final section consists of distribution maps for Europe and a separate set for Britain. These maps not only show the distribution of each species, but relative abundance and, in many cases, give an indication of whether the species is expanding its range or undergoing a decline. All the maps are keyed to species by numbers and are also explained at the foot of each page of maps with cross reference to the description. This is most useful since it enables one to turn directly from specific description to distribution map or vice versa with equal ease. I have a minor criticism that the area of colour on the maps of very local species is often so small that one needs to look very carefully to spot the real distribution, especially in artificial light. In one or two cases the dots used to indicate an isolated record are clearer than the thin coloured areas. See, for example, the British map for *Theba pisana* (No. 269, p. 287) where the St. Ives colony is more obvious than all those in South Wales put together, or compare the European map for *Catinella arenaria* (No. 19, p. 228) with that for *Cochlicopa nitens* (No. 24, same page).

The area covered extends from the Pyrenees in the southwest to Finland in the northeast, includes France except for the Mediterranean departments, the Low Countries, Germany, Scandinavia, the British Isles, and Iceland. As the preface states, this is the first snail guide to cover more than a national fauna since Ehrmann's work in the "Tierwelt MittelEuropas" which first appeared in 1933.

Missprints are very rare, but the explanation of plate 22, figs. 4a–c should be *Trissexodon constrictus*, not *T. constructus*. Altogether the book is excellent and modestly priced. Seldom can so much useful information have been included within such a small convenient handbook.

C.R.C.P.



# GROWTH AND FECUNDITY OF *PISIDIUM AMNICUM* (MÜLLER) (BIVALVIA: SPHAERIIDAE) IN THE TADNOLL BROOK, DORSET, ENGLAND

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(Read before the Society, 19 May 1979)

*Abstract:* In a chalk stream in southern England *Pisidium amnicum* (Müller) released one annual brood of young in May. A small proportion of the largest adults, surviving brood release, initiated a second brood during August. In the present study these adults died before the young were fully developed. It is suggested that an extended life cycle may occur in other habitats. A slow-growing embryo brood developed in a steadily increasing proportion of the adults from August to April. The number of embryo shells was related to adult shell length. Mean brood size was 13 individuals, with a maximum of 37 recorded from adults of 8.0 and 8.5 mm.

*Pisidium amnicum* (Müller) has a Palaearctic distribution and is common in Europe, north of the Alps and Pyrenees (Kuiper and Wolf, 1970). It has been recorded by Heard (1962) as an introduced species in North America. *P. amnicum* is the largest of the sixteen species of *Pisidium* currently recorded from the British Isles and, together with the other sphaeriids, is ovoviviparous, an unusual reproductive strategy among bivalves. The young are nurtured in marsupial brood sacs in the branchial chambers and released as immature adults.

Samples of *P. amnicum* were collected from the Tadnoll Brook (Nat. Grid. Ref. SY 796873), providing sufficient specimens for analysis of growth and fecundity, over a twelve month period. Changes in population structure were interpreted from measurement of the shells of adults and embryos.

## SAMPLING SITE

The Tadnoll Brook is a small chalk stream influenced, in its lower catchment, by drainage from heathland based on tertiary sediment deposits. The water has high levels of dissolved calcium carbonate (range 2.3–4.4 m Eq l<sup>-1</sup>), the water chemistry is described by Casey and Newton (1973). The mean annual flow at the sampling point is 0.6 m<sup>3</sup> s<sup>-1</sup>, the stream width being 3–5 m and depth 0.3–1.5 m. Extensive areas of sand are present, with deposits of fine silt and allochthonous leaf fragments associated with the roots of aquatic plants, principally *Potamogeton pectinatus* L. and *Myriophyllum* sp. Further details of the site are given by Pinder (1974).



## METHODS

A standard pond net with a mesh size of 1 mm (small enough to retain even the smallest free-living *P. amnicum*) was used to skim the top 20–30 mm of sediment. The bottom of the net was swirled on the water surface to reduce the volume of fine sediment. In the laboratory, *P. amnicum* were sorted and placed singly in glass vials. The animals were killed by warming the vials to 60° C for about two minutes, tap water was added and the soft tissues allowed to rot for one to three weeks, depending on the individual size. Shelled embryos, associated with the parent, were recovered. The shells were washed in alcohol and dried before being measured, using a stereoscopic microscope with a micrometer eyepiece.

## RESULTS

Growth of adults and their developing young was slow from October to April but a steady increase in the proportion of adults containing embryos occurred (Fig. 1). An increased rate of shell growth in April continued until August. It is clear that the small number of large adults in August and September, entering their second year of life, did not increase appreciably in length and were obscured as a group by the fast-growing cohort released in the preceeding May. The growth rate of embryos within the parent brood chambers accelerated in April and early May (Fig. 2), with the broods being released during late May or early June.

An attempt was made to eliminate the possible effect of staggered embryo formation, or premature release of young, on assessment of fecundity (Fig. 3). The relationship of the number of embryos to the length of the corresponding adult shell throughout the sampling period, irrespective of the effect of incomplete broods (Fig. 3, crosses), was compared with broods having embryos within certain size limits (Fig. 3, open circles) (0.3–0.8 mm shell length). The smallest free-living specimen found was 1.2 mm and the largest embryo within an adult was 1.4 mm shell length. The mean brood-size in April and early May was 13 embryos, the maximum being 37, present in only two adults of 8 mm and 8.5 mm shell length.

## DISCUSSION

Until recently the biology of *P. amnicum* has escaped the attention of workers in this field. This species has been briefly mentioned in earlier studies of the biology of *Pisidium* species, Meier-Brook (1970) quotes from Thiel (1928) and Odhner (1929), while Hadl (1972) also noted that young were released in spring and broods were not present in adults during the summer. More recently Danneel and Hinz (1976) described the biology of *P. amnicum* in Germany, confirming the absence of embryos in mid-summer and the release of one generation of young in late May and early June.

In the Tadnoll Brook, the one-year-old adults surviving brood release were obscured as a group in the autumn, by the faster-growing newly-recruited young released in May. It seems likely that the decreasing proportion of adults in the two largest size classes after August (Fig. 1), when no further recruitment is taking place, indicated their death. These adults initiated shelled embryos during August and September but no young were released before the following May.

A closely related species, *P. dubium* (Say), in Ore Creek, North America (Heard, 1965) had a three year life-span, producing a brood annually during May and June. Previous studies on *Pisidium* species suggest that life-cycles can be modified by the duration of the growing season in a particular habitat (Odhner, 1929; Heard, 1965; Ladle and Baron, 1969; Mitropol'skii, 1969,



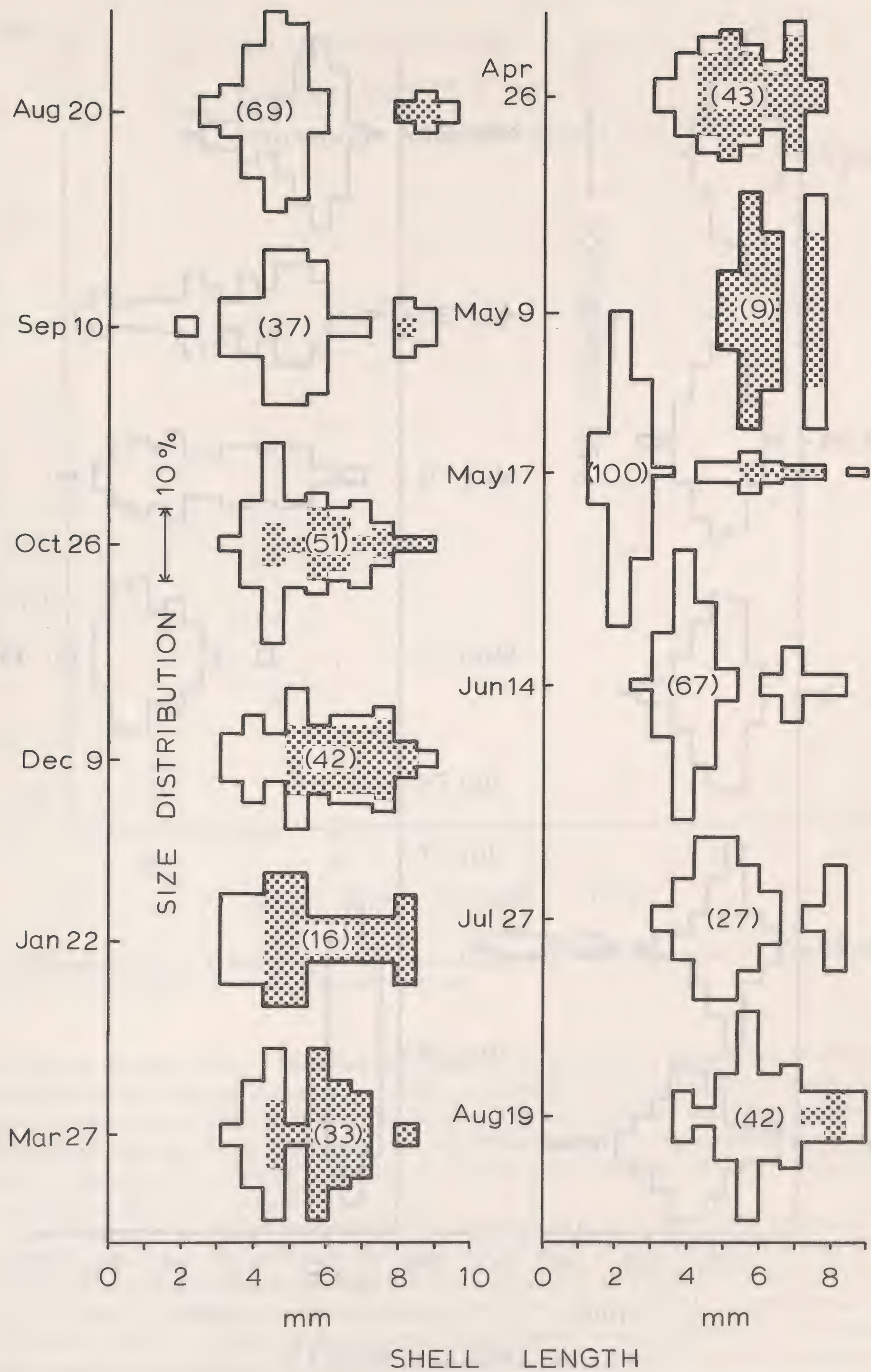


Fig. 1. Percentage size distribution of *P. amnicum*, hatched areas indicate the proportion bearing shelled embryos. Number of adults measured in parenthesis.



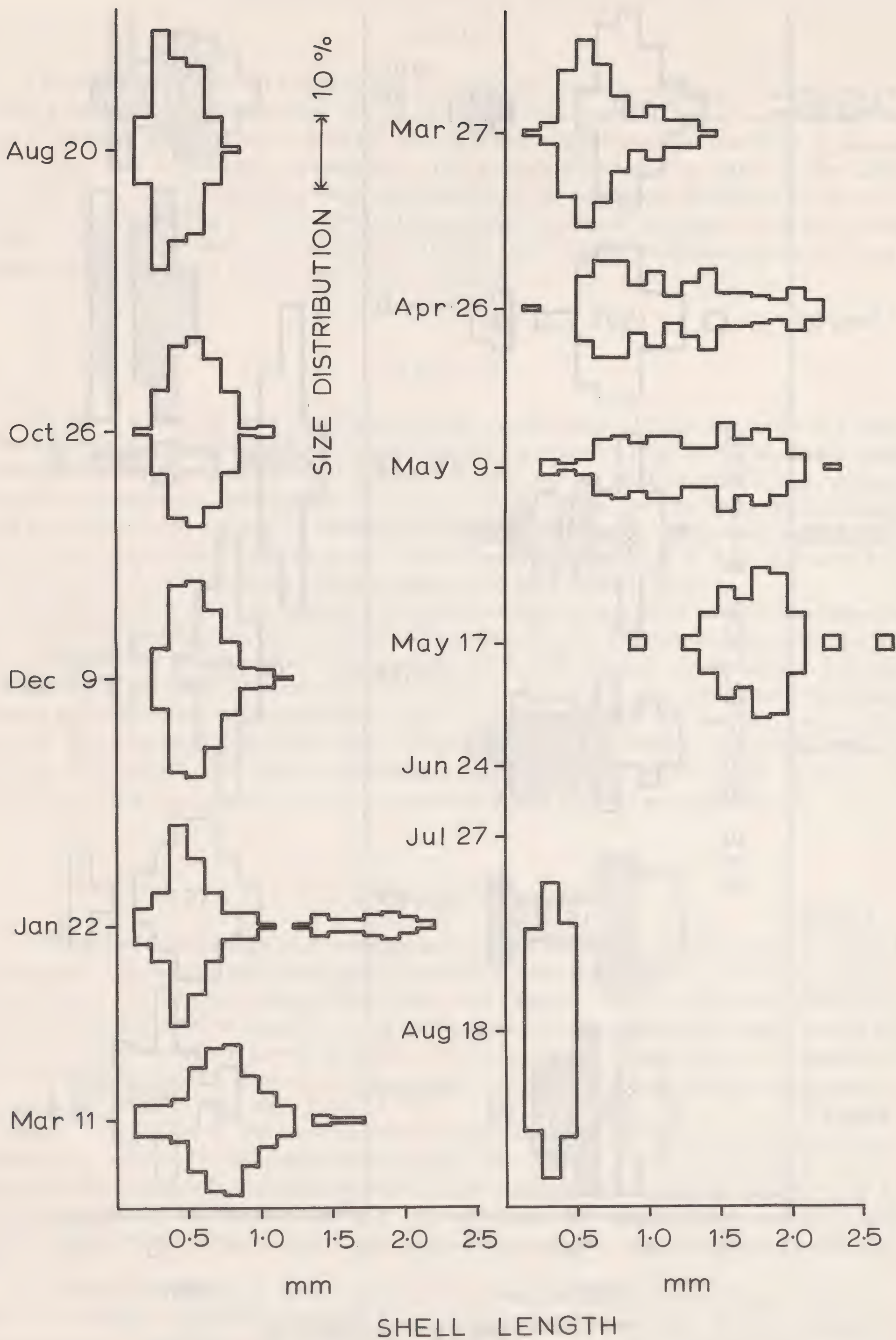


Fig. 2. Percentage size distribution of *P. amnicum* embryo shells, present in adults.



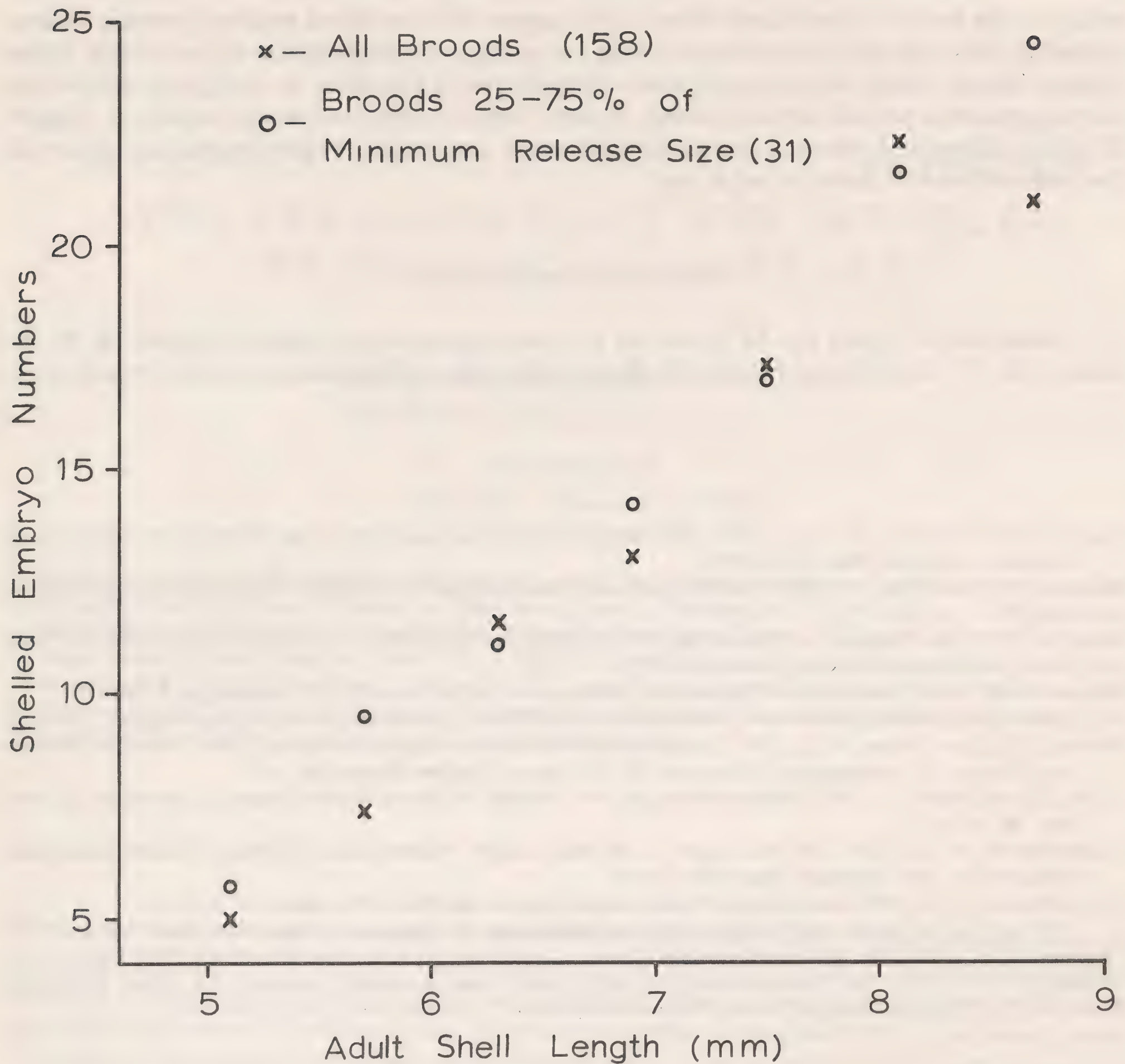


Fig. 3. Relationship of adult *P. amnicum* shell length to mean brood size. x – all broods included; o – restricted to broods with embryos within 25%–75% of the minimum release size.

1970; Meier-Brook, 1970). *P. amnicum* may succeed in releasing a further brood either in a habitat where the growing season is extended, as in southern parts of its range, or in a colder climate where an increased life-span could be advantageous to the survival of a population. An extended life-span in a more rigorous habitat would offset the effect of poor recruitment in some years. A reproductive strategy involving the compromise between increased life-span and reduced fecundity may operate.

The long period of shelled brood initiation in the adults may be accounted for by successive maturing of adults, as they reach the minimum size (4 mm) at which young are present. This continuing initiation of broods, through the winter, gives rise to a broad size-range of embryos between adults. There is a clear relationship between the number of embryos and the size of the adult shell (Fig. 3), but there is no evidence of additional young appearing in a brood after shelled embryos are present. Competition between embryos was found to occur in other species of *Pisidium* (Meier-Brook, 1970), with a proportion of embryos ceasing to grow and dying on



release of the brood. Danneel and Hinz (1976) suggest that the brood reaches a certain volume related to adult size and is then released, with young below a threshold size not surviving. In the Tadnoll Brook young were released over a short period in late May or early June, despite the varying gestation periods between broods. It may be speculated that the mechanism or 'trigger' for this synchronized release, is associated with water temperature or day-length, as well as with the ratio of brood volume to adult size.

## ACKNOWLEDGEMENTS

I would like to thank Dr. M. Ladle for his encouragement and advice, also Mr. R. H. K. Mann, Mr. T. Gledhill and Miss B. M. Baldock for their useful comments on the manuscript.

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*MARSTONIOPSIS SCHOLTZI* (A. SCHMIDT)  
AND *FERRISSIA WAUTIERI* (MIROLI)  
FROM HILGAY, NORFOLK.

R. C. PREECE AND R. D. WILMOT  
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(Read before the Society, 21 April 1979)

*Abstract:* The small hydrobiid prosobranch *Marstoniopsis scholtzi* (A. Schmidt) has hitherto been recorded in Britain only from canals in Lancashire and Cheshire and from timber ponds at Grangemouth in Stirlingshire. This restriction to artificial habitats has led to the suggestion that it must have been introduced from the Continent, where it is widespread. A colony is now reported from the Great Ouse at Hilgay in Norfolk; also present at the same locality is the limpet *Ferrissia wautieri* (Mirolli), discovered in Britain in 1977 and, like *Marstoniopsis*, known otherwise from man-made habitats only. The history of the discovery of *Marstoniopsis* in this country is reviewed, together with data on fossil occurrences; the evidence for its native status remains ambiguous.

A study of the bottom sediments and hydrogeology of the rivers of the Wash drainage basin by one of us (R.D.W.) has allowed examination of the Mollusca (by R.C.P.) present in grab-samples of sediment. It was thought that numerical information about freshwater bivalves, especially the genus *Pisidium*, could be related to sedimentological data (grain-size, water chemistry, hydrology). Gastropods were also common in the samples and this note records the occurrence of *Marstoniopsis scholtzi* (A. Schmidt) and *Ferrissia wautieri* (Mirolli) which are uncommon in Britain.

LOCATION AND HABITAT

Both species were present in a sample, collected in April 1978, which was obtained with a Van Veen grab from near the centre of the channel of the Great Ouse near Hilgay, Norfolk (TL599977). The river here is 45-50 m wide and 3-4 m deep with a bottom composed of very fluid silty-clay material. Using long term discharge values from Denver sluice, 5 km downstream, the average water velocity is estimated to be in the order of  $15 \text{ cm sec}^{-1}$ , although occasionally it may rise to  $1 \text{ m sec}^{-1}$ . Despite this relatively low velocity, the water is fairly well oxygenated. The Great Ouse and its tributaries drain the Chalk and the Chalky Boulder Clay and this is reflected in the mean calcium concentration of the water (153 ppm) and mean alkalinity (224 ppm  $\text{CaCO}_3$ ). During very low flow conditions some saline intrusion occurs at Denver sluice and although the molluscan assemblage shows no evidence of this reaching as far upstream as Hilgay, the mineralogy of the clay fraction suggests that estuarine material has been transported this far at some time.



In November 1978, further specimens of both species were taken with a net from among dead *Sparganium* which lined the banks of the river near the original sampling point. Shells of *M. scholtzi* had also been used by trichopteran larvae for the construction of their cases. Although fresh shells were found on both occasions, live snails of these species were not found.

## MOLLUSCA

The list of Mollusca present in the original grab-sample is given in Table 1. Only those specimens retained by a 30 B.S. mesh sieve (0.5 mm) have been counted. A distinction has been made between fresh material (specimens retaining some translucence and often with the periostracum intact) and dead shells (generally opaque and usually white and brittle). In addition to the species present in the original grab-sample, the following were seen in the field in November 1978: *Lymnaea truncatula* (Müller), *L. palustris* (Müller), *L. stagnalis* (L.), *L. auricularia* (L.), *Planorbis carinatus* Müller, *Planorbarius corneus* (L.), *Unio pictorum* (L.), *Anodonta cygnea* (L.), *Pseudanodonta complanata* (Rossmässler) (the last new to v.c. 28).

The presence of *Ferrissia wautieri*, a limpet newly discovered in Britain, is noteworthy. A single fresh specimen was present also in a sample taken from the Great Ouse at Great Barford, Bedfordshire (TL125510). Hitherto in Britain it was only known from lilly-ponds in greenhouses (Brown, 1977), and in man-made ponds in Sussex (Holyoak, 1978) and the Isle of Wight (Preece, unpublished).

## MARSTONIOPSIS SCHOLTZI IN BRITAIN

*Marstoniopsis scholtzi* was first discovered living in Britain in April 1900 by Fred Taylor in the canal near Fairfield Locks, Droylesden, Lancashire. Taylor also found it in September of the same year in a short arm of the Peak Forest Canal at Dukinfield, Cheshire and at intervals along the canal as far as Woodley (Jackson and Taylor, 1904). E. A. Smith gave the name *Paludestrina taylori* to these specimens which were sent to him in October 1900 (Smith, 1901). Smith does not figure his new species; Jackson and Taylor's illustration is a general drawing that cannot be referred to any one specimen. Consequently it is worthwhile figuring two presumed syntypes of *Paludestrina taylori* collected by Taylor and registered by the British Museum (Natural History) in 1901 (Figure 1C and D).

Jackson and Taylor (1904) commented on the similarity between these specimens and '*Bithynella steeni*' (= *scholtzi*) and Smith himself thought it impossible to distinguish them, but preferred to retain his name until detailed anatomical studies were made. Jackson and Taylor gave further details of the biology of *taylori* and concluded that in both shell character and in its oviparous habit *taylori* should be referred to the North American genus *Amnicola*. Altena (1936) reviewed the systematic positions of *steinii* and *taylori* concluding that they were synonymous and erected a new genus *Marstoniopsis* (with *steinii* as the type species) since he could not refer the species to either *Hydrobia*, *Bythinella*, *Amnicola* or its subgenus *Marstonia*. All authorities now agree that *Hydrobia steinii* Martens, 1858 is a junior synonym of *Hydrobia scholtzi* A. Schmidt, 1856 and that the British species should be called *Marstoniopsis scholtzi* (A. Schmidt) (Kerney, 1976). A full synonymy together with further details of its biology and occurrence, is given by Boeters (1973).

Although *M. scholtzi* is widespread in Europe, extending westwards as far as Scandinavia and the Low Countries (Boeters, 1973), the cluster of sites in Lancashire and Cheshire remained the only British localities until its discovery in 'ponds used for seasoning timber at Grangemouth, Stirlingshire' (Waterson, 1934). Both here and at its original British sites it was abundant among decaying reed meadow grass, *Glyceria maxima* (Hartmann).



## MARSTONIOPSIS AND FERRISSIA IN NORFOLK

TABLE 1

Mollusca present in a grab-sample from the mid-channel of the Great Ouse at Hilgay  
(April 1978). Dry weight of >0.5 mm fraction = 5.5 g.

|                                            | Dead      | Fresh | Total |
|--------------------------------------------|-----------|-------|-------|
| <i>Viviparus viviparus</i> (L.)            | fragments | —     | +     |
| <i>Valvata cristata</i> Müller             | 21        | 3     | 24    |
| <i>Valvata piscinalis</i> (Müller)         | 23        | 34    | 57    |
| <i>Valvata opercula</i>                    | —         | —     | 7     |
| <i>Potamopyrgus jenkinsi</i> (E. A. Smith) | 268       | 306   | 574   |
| <i>Marstoniopsis scholtzi</i> (A. Schmidt) | 4         | 3     | 7     |
| <i>Bithynia tentaculata</i> (L.)           | 28        | 14    | 42    |
| <i>Bithynia leachii</i> (Sheppard)         | 11        | 6     | 17    |
| <i>Bithynia opercula</i>                   | —         | —     | 65    |
| <i>Physa fontinalis</i> (L.)               | —         | 2     | 2     |
| <i>Lymnaea peregra</i> (Müller)            | 3         | 5     | 8     |
| <i>Anisus vortex</i> (L.)                  | 3         | —     | 3     |
| <i>Bathyomphalus contortus</i> (L.)        | 3         | 2     | 5     |
| <i>Gyraulus albus</i> (Müller)             | 13        | 11    | 24    |
| <i>Armiger crista</i> (L.)                 | 9         | 5     | 14    |
| <i>Hippeutis complanatus</i> (L.)          | 8         | 4     | 12    |
| <i>Ancylus fluviatilis</i> Müller          | —         | 12    | 12    |
| <i>Ferrissia wautieri</i> (Mirolli)        | 2         | 4     | 6     |
| <i>Acroloxus lacustris</i> (L.)            | 5         | 7     | 12    |
| <i>Unio tumidus</i> Philipsson             | 1         | 2     | 3     |
| <i>Anodonta anatina</i> (L.)               | —         | 2     | 2     |
| <i>Sphaerium corneum</i> (L.)              | 6         | 3     | 9     |
| <i>Sphaerium lacustre</i> (Müller)         | 5         | 7     | 12    |
| <i>Pisidium amnicum</i> (Müller)           | —         | 1     | 1     |
| <i>Pisidium casertanum</i> (Poli)          | 1         | 1     | 2     |
| <i>Pisidium subtruncatum</i> Malm          | 17        | 16    | 33    |
| <i>Pisidium henslowanum</i> (Sheppard)     | 3         | 6     | 9     |
| <i>Pisidium nitidum</i> Jenyns             | 14        | 10    | 24    |
| <i>Pisidium pulchellum</i> Jenyns          | —         | 1     | 1     |
| <i>Pisidium moitessierianum</i> Paladilhe  | 2         | —     | 2     |
| <i>Dreissena polymorpha</i> (Pallas)       | 5         | 9     | 14    |

Note that the totals given for bivalves refer to the number of individual valves.

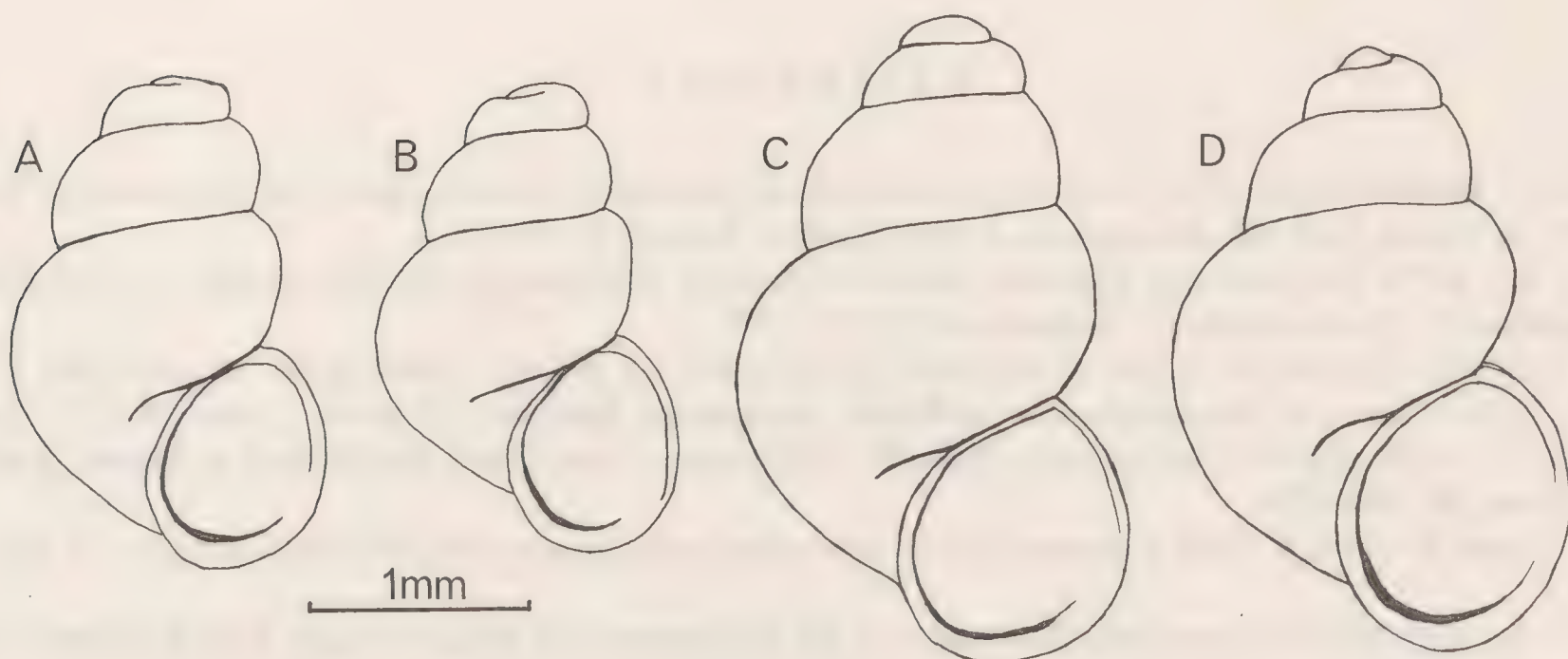


Fig. 1. *Marstoniopsis scholtzi* (Schmidt) A Hilgay, Norfolk; B County Hall, Waterloo, London (fossil; BMNH GG13340); C, D Syntypes of *Paludestrina taylori* E. A. Smith, Cheshire (BMNH 1901.3.28. Nos. 30 and 32).



The occurrence of *M. scholtzi* in artificial habitats in Britain has led to the suggestion that it must be a Continental introduction. Clearly the Lancashire colonies must post-date the construction of canals there during the Industrial Revolution, but the origin and status of these colonies remains obscure. At Hilgay *M. scholtzi* was unexpected considering the apparent contrast between the Lancashire canal sites and that of the Great Ouse. However it can easily be overlooked amongst the great numbers of the superficially similar *Potamopyrgus jenkinsi* and might well be present at other sites in eastern England.

*M. scholtzi* was recognized as a fossil in Britain long before it was discovered living. It is known from the Cromerian and Ipswichian interglacials, but not from the Hoxnian (Kerney, 1977). Ellis (1951) cites *M. scholtzi* as a Postglacial (Flandrian) fossil from Huntingdon (v.c. 31), Cambridge (v.c. 29) and Surrey (v.c. 17). The record for the first two vice-counties is derived from Kennard and Woodward (1922) who list '*Bythinella* sp' from alluvial deposits containing 'mediaeval glass' from an island in the Great Ouse at St. Ives, Huntingdonshire (TL310715), some 35 miles (56 km) upstream from Hilgay. The single specimen cannot be located in Kennard's collection from this site in the British Museum (Natural History), nor is it referred to in his notebooks either under species or locality headings. In view of this it seems wise to reject this record. The Surrey record is based on an undoubted specimen (BMNH registration no. GG13340) collected in 1919 from the side of County Hall, Waterloo (TQ 3079) '8' below surface of river mud and 10' above London Clay at the same level and near to Roman boat in London Museum' (Kennard MS). The exact age of the deposit, which contains a rich freshwater mollusc assemblage, is not known although it is almost certainly post-Roman. Kennard was obviously uncertain about his identification for notebook entries are variously given as '*Bythinella steinii*' and '*P. ventrosa*' although the tube containing it is labelled '*minuta*'. The specimen, however, compares well with *M. scholtzi* from Hilgay (cf. Fig. 1A and B). Whether it is safe, on the basis of this specimen, to infer that *M. scholtzi* is native to Britain, is questionable.

#### ACKNOWLEDGEMENTS

This work was conducted while R.D.W. was in receipt of a N.E.R.C. Research Studentship and during the tenure of an 1851 Research Fellowship by R.C.P. We would also like to thank Dr. M. P. Kerney for his help and Dr. P. B. Mordan and Mr. J. Cooper of the British Museum (Natural History), for the loan of specimens.

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THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND  
INCOME AND EXPENDITURE ACCOUNTS FOR THE YEAR ENDED 31st DECEMBER, 1978

|                                    | £   |     | £         |                                       | £         |
|------------------------------------|-----|-----|-----------|---------------------------------------|-----------|
| Publications:                      |     |     |           |                                       |           |
| News Letter ...                    | ... | ... | 999.61    | Fees and Subscriptions:               |           |
| Student Papers ...                 | ... | ... | 69.83     | Membership Fees ...                   | 2,596.71  |
|                                    |     |     |           | Subscriptions ...                     | 1,280.85  |
|                                    |     |     |           | Entrance Fees ...                     | 24.50     |
| Journal:                           |     |     |           |                                       | <hr/>     |
| Volume 29 No. 5                    | ... | ... | 1,513.67  | Grant from World Wildlife Fund        | 3,902.06  |
| Volume 29 No. 6                    | ... | ... | 1,945.63  | Donations ...                         | 300.00    |
|                                    |     |     | <hr/>     |                                       | 100.06    |
|                                    |     |     | 3,459.30  |                                       |           |
| Census Cards and Instructions ...  | ... |     |           | Sales:                                |           |
| Cost of Atlas, Postage and Packing | ... |     | 266.98    | Atlas ...                             | 299.60    |
| Printing, Stationary and Postage   | ... |     | 22.72     | Advertising ...                       | 4.00      |
| Officers' Expenses...              | ... |     | 553.05    | Journals ...                          | 56.58     |
| Subscriptions                      | ... |     | 109.26    | Student Papers ...                    | 53.55     |
| Meetings ...                       | ... |     | 14.00     | News Letter ...                       | 4.99      |
| Sundry Expenses ...                | ... |     | 66.20     | Sundries ...                          | 21.00     |
|                                    |     |     | <hr/>     |                                       | <hr/>     |
|                                    |     |     | 2.65      |                                       | 439.72    |
|                                    |     |     |           |                                       |           |
|                                    |     |     | 5,563.60  | Investment Income:                    |           |
|                                    |     |     |           | General Account ...                   | 874.49    |
| Net Surplus..                      | ... | ... | 259.95    | Life Members Fund ...                 | 207.22    |
|                                    |     |     | <hr/>     | Reserve and Research Fund ...         | 118.06    |
|                                    |     |     | £5,823.55 |                                       | <hr/>     |
|                                    |     |     |           | Transfer to Reserve and Research Fund | 1,199.77  |
|                                    |     |     |           |                                       | <hr/>     |
|                                    |     |     |           |                                       | 118.06    |
|                                    |     |     |           |                                       | <hr/>     |
|                                    |     |     |           |                                       | 1,081.71  |
|                                    |     |     |           |                                       | <hr/>     |
|                                    |     |     |           |                                       | £5,823.55 |
|                                    |     |     |           |                                       | <hr/>     |



BALANCE SHEET AS AT 31st DECEMBER, 1978

|                                   |     |   |                 |                                     |     |   |                   |
|-----------------------------------|-----|---|-----------------|-------------------------------------|-----|---|-------------------|
| Fees and Subscriptions in Advance | ... | £ |                 | Cash at Bank: Current Account..     | ... | £ | 263.86            |
| Life Membership Fund ...          | ... |   | 392.27          | Deposit Account ..                  | ... |   | 715.98            |
| Reserve and Research Fund         | ... |   | 1,910.00        | Post Office Savings                 |     |   |                   |
|                                   |     |   | 1,206.26        | Bank ...                            | ... |   | 2,872.33          |
|                                   |     |   |                 |                                     |     |   | <u>3,852.17</u>   |
| <i>Capital Account</i>            |     |   |                 |                                     |     |   |                   |
| Balance Brought Forward           | ... |   | 8,060.47        |                                     |     |   |                   |
| Add Surplus for the Year          | ... |   | 259.95          |                                     |     |   |                   |
|                                   |     |   | <u>8,320.42</u> |                                     |     |   |                   |
| <i>Investments</i>                |     |   |                 |                                     |     |   |                   |
|                                   |     |   |                 | £400 5% Treasury Stock 1986/89      | ... |   | 344.00            |
|                                   |     |   |                 | £500 5¾% Deb. Stock Mersey Docks    |     |   |                   |
|                                   |     |   |                 | & Harbour Board 1980/82..           | ... |   | 222.29            |
|                                   |     |   |                 | 2,514 Units M. & G. Dividend Fund   |     |   | 1,522.06          |
|                                   |     |   |                 | £400 12½% Loan City of Norwich      | ... |   | 400.00            |
|                                   |     |   |                 | £800 5½% Loan London County         |     |   |                   |
|                                   |     |   |                 | Council.                            | ... |   | 769.20            |
|                                   |     |   |                 | 1,620 Scot Income Units             | ... |   | 892.95            |
|                                   |     |   |                 | £875 Spillers 7% Deb. Stock 1978/83 |     |   | 753.82            |
|                                   |     |   |                 | £500 Manchester Corporation Loan    |     |   | —                 |
|                                   |     |   |                 | £700 Bury 12¼% Loan.                | ... |   | 700.00            |
|                                   |     |   |                 | £800 15½% Treasury Stock 1998       | ... |   | 768.00            |
|                                   |     |   |                 | £95.68 Subordinated Loan Stock      |     |   |                   |
|                                   |     |   |                 | Mersey Docks & Harbour Board ...    |     |   | 95.68             |
|                                   |     |   |                 | 104 10p Ordinary Shares Mersey      |     |   |                   |
|                                   |     |   |                 | Docks & Harbour Board               | ... |   | 10.40             |
|                                   |     |   |                 | £2,340 7¼% Whitbread Stock 1995/99  |     |   | 1,498.38          |
|                                   |     |   |                 |                                     |     |   | <u>7,976.78</u>   |
|                                   |     |   |                 |                                     |     |   | <u>£11,828.95</u> |

MARJORIE FOGAN,  
*Hon. Treasurer.*

L. LLOYD-EVANS }  
Wm. F. EDWARDS } *Hon. Auditors.*

28th February, 1979



# PROCEEDINGS OF THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

## TREASURER'S REPORT, 1978

In comparison with the previous year there is little change in many items, as the income from Members and Subscribers, donations and investments is much as it was. There is a large decrease in sales, but 1977 was an exceptional year in that it saw very large sales of the newly-published *Atlas*. There has been a much smaller demand in 1978, with consequent lower income.

The Society is grateful to the World Wild Life Fund for a grant of £300. This was for the purpose of printing new cards and instructions for the Census, and to provide for their postage.

There has been a very considerable rise in the costs of the *Journal of Conchology*. While this is, in the main, a result of the constant increase in the cost of printing it should be remembered that it also includes the additional cost of the index and title-page for Vol. 29.

Our investment in £500 Manchester City 13½% Loan was repaid on 25th March 1978, and on 7th April this was reinvested, with the addition of a further £998.38, in £2,340 7¼% Whitbread Stock 1995/99 at £1,498.38 for the benefit of the General Account.

The accounts for 1978 show a small profit, but with increasing costs and a decreasing demand for the *Atlas* there is likely to be a deficit in 1979, although every effort will be made to keep this to a minimum. Your Council has therefore decided that it is necessary to recommend increases in the subscription rates, and these are to be the subject of a Special General Meeting.

19 Members and 4 Junior Members are in arrears with 1978 annual subscriptions. All Members are reminded that no further publications for 1979 will be sent to Members whose current subscriptions remain unpaid, although any publications which have been withheld will be dispatched upon receipt of the arrears.

MARJORIE FOGAN  
*Hon. Treasurer.*

## REPORT OF THE COUNCIL, 1978-79

*Membership.* It is with regret that the Society has to report the deaths of the following Members:- The Rt. Hon. the Earl of Cranbrook, who joined in 1969; Captain M. W. Hartley, who joined in 1976; Mr. P. H. Hodgson, who joined in 1969; Mrs. E. Hole, who joined in 1966; Dr. J. W. Jackson, who joined in 1901; Mr. J. Sofianos, who joined in 1977 and Mr. J. Summerton, who joined in 1965.

Total Membership now stands at 605 Members, comprised of the following categories: Full Members 538, of whom 32 are Life Members; Family Members—40, of whom 4 are Life Members; Junior Members—24 and Honorary Members—3. During the year 31 Members resigned and 32 were struck off for non-payment of subscriptions. 58 new Members were elected.

*Subscribers.* 160 Subscribers took 172 subscriptions to the *Journal of Conchology*, a loss of three subscribers on 1977. There were 12 subscriptions to the *Conchologists' Newsletter* and Papers for students.

*Meetings.* Six ordinary meetings were held during the year in the British Museum, Natural History and one Annual General Meeting. In October 1978 we changed our meeting venue from the *Conversazione Room* to the *Demonstration Room* in the Museum, when because of increased hiring charges, it no longer became economic to use the *Conversazione Room*. Although no tea facilities are available in the new room, the acoustics are greatly improved and a permanent projection screen is available with a projector. This makes the viewing of slides much clearer and one is able to hear the Lecturer without undue difficulty.

*Field Meetings.* Nine field meetings were held during 1978 as follows: 2nd April, Foulness Is. 5th-7th May, Rhosilli, Gower. 28th May, Nature Reserves in S.E. Essex. (Joint meeting with the Basildon N.H.S.). 10th June, Ipswich, Suffolk. (Joint meeting with the Ipswich Geological Group). 25th June, Joint meeting with the Northampton N.H.S. 15th July, Rye Harbour, Sussex. 8th September Dover, Kent (Joint meeting with the Kent Field Club). 23rd September E. Leicestershire. 22nd October Bedfordshire. Nine further meetings were also held in the northwestern area.



## PROCEEDINGS

Thanks are due to the following for leading these meetings: Mrs. M. Fogan, Dr. Joan Llewellyn Jones, Mrs. C. J. Pain, Mrs. E. B. Rands, Dr. P. F. Lingwood, Dr. M. P. Kerney, and Messrs I. M. Evans, J. Llewellyn Jones, R. A. D. Markham, G. H. Osborn, and D. R. Worth.

*Publications.* Two parts of the Journal of Conchology were issued, volume 29, parts 5 and 6 as well as the quarterly Conchologists' Newsletters.

## RECORDER'S REPORT: NON-MARINE MOLLUSCA

### A. GRID MAPPING

Quiet, steady progress is being maintained in completing the 10-kilometre square coverage of the British Isles. Tetrad ( $2 \times 2$  km square) surveys are also well advanced in a few English counties, notably Isle of Wight (v.c. 10), Kent (15 and 16), Surrey (17), Oxford (23), Bedford (30) and Northampton (32).

### B. VICE-COUNTY RECORDS

The following new records have been verified since the last Report (*J. Conch., Lond.* **29**, p. 371). Unless stated otherwise, the date of collection was 1978-79.

Note that a map allowing easy correlation between vice-counties and grid squares is included in the set of transparent overlays recently published by BRC for use with all distribution atlases, including our own.

Cornwall West (1): *Cecilioides acicula*, St Erth (10/5535), J. Humphreys.

Devon North (4): *Testacella scutulum*, Braunton (21/4835), Miss M. Jaques.

Isle of Wight (10): *Valvata cristata*, Barton Manor (40/5294); *Ferrissia wautieri*, Parkhurst (40/4991), R. C. Preece.

Hants South (11): *Boettgerilla pallens*, Buriton (41/7320), A. J. Rundle.

Sussex East (14): *Ferrissia wautieri*, Barcombe Cross (51/4218), D. T. Holyoak.

Surrey (17): *Boettgerilla pallens*, Petersham (51/1773), A. J. Rundle.

Suffolk East (25): *Pisidium moitessierianum*, R. Waveney, North Cove (62/4691), D. C. Long.

Norfolk West (28): *Marstoniopsis scholtzi*, *Ferrissia wautieri*, *Pseudanodonta complanata*, R. Ouse, Hilgay (52/5997), R. C. Preece and R. D. Wilmot.

Bedford (30): *Ferrissia wautieri*, R. Ouse, Great Barford (52/1251), R. C. Preece and R. D. Wilmot.

Radnor (43): *Pisidium amnicum*, R. Wye, Llowes (32/1942), S. P. Dance, 1973.

Leicester (55): *Boettgerilla pallens*, Hinkley (garden; 42/4392), G. Riley.

Chester (58): *Boettgerilla pallens*, Little Neston (garden; 33/2977), C. R. C. Paul; *Limax pseudoflavus*, West Kirby (33/2286), I. D. Wallace.

Northumberland South (67): *Acicula fusca*, Plessey Woods (45/2379), B. Colville.

Cheviot (68): *Limax pseudoflavus*, Berwick on Tweed (46/0052), I. D. Wallace.

Westmorland (69): *Catinella arenaria*, *Vertigo geyeri*, Tarn Moor, Orton (35/6707), B. Coles and B. Colville, 1974 and 1978.

Ayr (75): *Aplexa hypnorum*, Stevenston (26/2641), M. Sinclair, 1975.

Aberdeen South (92): *Gyraulus laevis*, Loch Davan (38/4400), M. W. Young.

Westernness (97): *Pisidium conventus*, Loch Morar (17/79), R. S. Grinvalds.

Main Argyll (98): *Acicula fusca*, Minard Point (17/8123), A. J. Rundle.

South Ebudes (102): *Acicula fusca*, Colonsay (16/3996); *Pisidium subtruncatum*, *P. nitidum*, Colonsay (16/3995); *Pisidium lilljeborgii*, *P. hibernicum*, Loch Fada, Colonsay (16/3996), all A. J. Rundle.

Clare (H 9): *Anodonta anatina*, Scarriff Bay, Lough Derg (R 7484), H. W. Dietrich, 1975.

Tyrone (H 36): *Pyramidula rupestris*, Castlederg (H 2684), R. Anderson.

There have been several important finds this year. Outstanding is the discovery of the glacial relicts *Vertigo geyeri* and *Catinella arenaria* in a calcereous fen in Westmorland (*J. Conch., Lond.* **30**, p. 99). This is the first British record of living *V. geyeri*, and only the second of *C. arenaria*.

The freshwater limpet *Ferrissia wautieri* (family Ancyliidae), a species recognized in this country only in 1977 (*Newsletter* no. 62: 28; *J. Conch., Lond.* **29**, p. 349), has been found in four vice-counties. Its superficial resemblance to *Acroloxus lacustris* has probably caused it to be overlooked; nevertheless, it cannot be very common, as a search through the collections of British *Acroloxus* and *Ancylus* in the BMNH failed to reveal further specimens. The Norfolk habitat for *Ferrissia* also yielded *Marstoniopsis scholtzi*, a doubtfully native British species previously known only from canals round Manchester and a timber pond at Grangemouth (*J. Conch., Lond.* **30**, p. 135).



A single living specimen of *Pisidium conventus* was dredged from a depth of 300 m in Loch Morar, Inverness-shire. Loch Morar is by far the deepest body of freshwater in the British Isles and one of the deepest in Europe.

Among the slugs, several more sites for *Boettgerilla pallens* have been found. *Limax pseudoflavus* (= *L. grossi* auctt.), a species common in Ireland, has been verified from Cheshire and Northumberland. The distributions of these two recently recognized species are summarized in *Newsletter* no. 69, p. 140.

M. P. KERNEY

## RECORDER'S REPORT: MARINE MOLLUSCA

### A. PRELIMINARY ATLAS

During summer 1978 I was approached by Roger Mitchell of Nature Conservancy Council, to cooperate in the production of a preliminary atlas consisting of twenty species. After some discussion two chitons, nine gastropods, one scaphopod, five bivalves and three cephalopods were agreed upon. The list was sent to each area representative with requests for 'spot' locations for each of the species recorded in his/her area. The response was gratifyingly swift and by the winter all the data were in. Since that time construction of suitable maps for marine recording has gone ahead steadily and it is hoped to have the 'mini-atlas' ready for distribution soon.

Dennis Seaward has accepted the post of Marine Recorder as from March 1979, following my resignation. I wish him, and all of you, good luck.

C. P. PALMER

### B. RECORDING

To date (May) I have received reports for 1978 from the representatives for sea areas 2 (Sutherland; R. G. Meiklejohn), 16 (Portland; D. R. Seaward), 18, 19 and 20 (Plymouth, Scilly Isles, N. Cornwall; Mrs. S. M. Turk) and 29a (Antrim; M. Brisco). For sea area 25 (Solway), N. Hammond has sent me a copy of his paper *Solway molluscs* which covers shore and inshore waters (10 km squares) in his area. In future, area representatives' detailed reports will be published in the *Newsletter* and I hope that some of them will appear in the September issue.

### C. AREA REPRESENTATIVES

Some changes have occurred and I hope to publish an up to date list in the September *Newsletter*.

### D. GENERAL

I have arranged a meeting of area representatives to be held on 2 June, 1979 at the South Shields Museum, by kind permission of F. Woodward, area representative for sea area 9 (Northumberland), who is Principal Keeper of Natural Sciences at the Museum. A report of this meeting will subsequently be published in the *Newsletter*.

D. R. SEAWARD



## INSTRUCTIONS TO AUTHORS

Authors of papers submitted for publication in the *Journal of Conchology* are urged to pay careful attention to the following notes. Any author who has difficulty in complying with these requests, or has queries concerning manuscripts, should consult the Hon. Editor **before** submitting a manuscript.

1. Manuscripts should be sent to the Publications Committee, c/o Dr. M. P. Kerney, Dept. of Geology, Imperial College, London, SW7 2AZ.

2. **Two** copies of all text and illustrations should be submitted. (A few years ago the entire copy for one issue of the *Journal* was lost in a mail robbery!). Authors are strongly recommended to retain a further copy for proof correction.

3. The text should be **fully revised**, typed **double spaced**, with wide margins (at least 1 inch), pages numbered consecutively and should conform in style to recent issues of the *Journal*. Titles should be concise and apposite, address(es) of author(s) should follow the title. Linear measures and weights should be metric and authorities for specific names should be given when first mentioned. Location of voucher material should be stated wherever possible. A brief, but informative, abstract should precede the main text.

4. Originals of text-figures should be  $1\frac{1}{2}$ –2 times the final size but should not exceed 25 by 36 cm. They should be drawn in Indian ink on clean ground, numbered consecutively, and referred to in the text as “Fig. 1” etc. Authors are strongly urged to construct text-figures so as to make full use of the page width and to submit a copy reduced to final (published) size wherever possible. Lettering should be legible and not less than 1 mm high after reduction.

5. Plates should only be used when essential and **must** not exceed 19.5 by 15 cm. They should utilise quality prints showing fine detail and moderate contrast. As far as possible prints on one plate should be matched for contrast and brightness. Authors are urged to make fullest use of plate space due to the high cost of printing plates. In the text the explanations of text-figures and plates should follow the references.

6. Tables should be concise, fit into the text and table headings should be self explanatory wherever possible. Tables are not printed “boxed”.

7. All papers referred to in the text (including synonymy lists) should be listed alphabetically by author's surnames at the end of the text under “References”. For books give author's name, initials, date, full title, pages, plates and place of publication.

*e.g.*

ELLIS, A. E. 1926. *British snails. A guide to the non-marine Gastropoda of Great Britain and Ireland, Pliocene to Recent*. 275 pp., 14 pls., Oxford.

BROWN, P. and STRATTON, G. B. (Editors). 1965. *World list of scientific periodicals published in the years 1900–1960*. (4th Ed.) 3 vols. London.

For periodicals give full title of the article, title of the periodical abbreviated according to the World List (4th Ed.), volume number, page numbers and plates.

*e.g.*

WOODWARD, F. R. 1965. Monograph of the British Lower Tertiary Unionidae, with descriptions of three new species. *J. Conch., Lond.* **25**: 316–330, pls. 22–27.

GOULD, S. J. 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail *P. (Poecilozonites)* in Bermuda. *Bull. Mus. comp. Zool. Harv.* **138**: 407–532, 5 pls.

8. Authors may obtain copies of all papers (other than brief notes) at cost price if ordered from printers (address: Messrs. Willmer Brothers Ltd., 62–68 Chester Street, Birkenhead, England) when galley proofs are returned.



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## CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

Annual subscriptions (for rates see inside front cover) fall due on 1st January. Members whose current subscriptions are unpaid will not receive any of the Society's publications. Please ensure that remittances cover the total amount due. Receipts will only be issued on request, accompanied by a stamped addressed envelope (overseas Members may add 10p to the amount sent). Cheques etc. should be made payable to the *Conchological Society of Great Britain and Ireland* and not to any individual officer by name.

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COVER DESIGN: *Muricanthus nigratus* (Philippi) by D. G. Reid.

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## NOTICE

### Payment by Overseas Members

Overseas members are reminded that all monies due to the Society are payable in sterling.

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# STUDIES ON THE REPRODUCTIVE BIOLOGY OF GASTROPODS: PART III. CALCIUM PROVISION AND THE EVOLUTION OF TERRESTRIAL EGGS AMONG GASTROPODS

ALEX S. TOMPA

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(Read before the Society, 20 October, 1979)

*Abstract:* Perhaps the most obvious specialization of molluscs is their ability to form a calcium carbonate shell which encloses and protects the body. In gastropods, shell formation and calcification begin while the embryo is still inside the egg, so that by the time of hatching the neonate has a rather well-formed body shell, the protoconch. Gastropod eggs which are laid in an aquatic environment have direct access to calcium from the surrounding waters. Eggs laid in a terrestrial environment, however, do not have direct access to calcium if the eggs are merely dropped into a hole in the ground or left in leaf litter, the two most common sites for land snails. Instead, the parent must make some modifications of egg composition or laying habit to make available the large amounts of calcium needed during embryonic development.

Calcium provision for the egg has been approached by a number of different ways; what they all have in common is that calcium salts are always deposited on the outside of the egg but do not occur in the egg albumen. It is presumed that a high concentration of calcium in the egg albumen is toxic to the zygote. The whole range of the methods of supplying calcium for eggs is surveyed. Some land snails merely coat each egg with calcium rich soil, either directly with the foot or by means of (soil) faecal pellets appressed to the egg shell surface. Other land snails have specialized pouches in the reproductive tract where calcium is kept for coating each egg or capsule. The most successful land snails, the Stylommatophora, take calcium from stores in the digestive gland and/or body shell and transport this as ionic calcium through the blood, across a specialized uterine epithelium to the formative eggs where calcite precipitates.

The present work involves the examination of the eggs of a soleoliferan slug, *Veronicella ameghini* Gambetta. The egg surface is lightly sprinkled with spherules of calcium carbonate, and the embryo is found to resorb egg shell calcium during development. Faecal strands incorporated into the egg surface are another source of calcium.

Finally, a list of gastropod families known to be terrestrial is presented with a suggestion that the eggs be examined to see if they also support the hypothesis presented here: that successful terrestrial colonization by gastropods involves an ability by the parent to supply the eggs with a large amount of calcium.

Many evolutionary lines of gastropods have become terrestrial independently (Morton, 1967; Solem, 1974). To date, there has been no general hypothesis about the types of eggs and the method of their formation in the transitional stages between aquatic (both freshwater and marine) and terrestrial gastropods. In this paper, I suggest that provision of large amounts of calcium around eggs, usually as one of the relatively insoluble salts of calcium carbonate, was one of the major steps in the evolution of truly terrestrial eggs in such diverse gastropods as land pulmonates, land archeogastropods, mesogastropods and soleoliferans. Calcium is a well known limiting factor in the ecological distribution of land pulmonates and land prosobranchs



(Boycott, 1934; Lais, 1943), but the importance of this element has been discussed only with respect to the adult organism.

Because aquatic environments are generally rich in calcium (especially the ocean, 400 ppm in  $\text{Ca}^{++}$ ), directly accessible to the inside of eggs by diffusion, freshwater and marine gastropods are not expected to coat their eggs with calcium salts unless the snails leave the water to deposit their eggs *completely above* the highest water level, tides, or spray zone. In order to form the cleidoic eggs (cleidoic eggs are those which are supplied with everything the embryo needs, except oxygen from the air; this word means 'closed box', literally) of land snails – at least some land snail eggs are known to be cleidoic – other essential ions need also to be included in the egg by the parent, but usually only in trace or minor amounts. The large amount of calcium needed for gastropod development makes this element a critical limiting factor in land colonization. (It is of course theoretically possible to evolve eggs whose embryos are dependent on less and less calcium, resulting in slug-like animals at the time of hatching, and this concept is also examined.)

The opportunity to test this line of reasoning arose when the land soleoliferan, *Veronicella ameghini* Gambetta, was obtained from northern Florida and was found to reproduce in the laboratory. Although eggs of this genus (Vosseler, 1912) and adults of this same species (Peterellis and Dundee, 1969) have been examined before, detailed observations on egg laying, egg structure and calcium content are lacking.

This study is therefore divided into two sections: 1) the first section describes the morphology and calcium content of the egg of this soleoliferan and 2) the second section examines the hypothesis that terrestrial colonization by gastropods has resulted in independent ways of providing large amounts of calcium to the embryo inside the egg.

#### MATERIALS AND METHODS

The genus *Veronicella* is a member of the widely distributed tropical and subtropical family Veronicellidae (formerly Vaginulidae). These land slugs were at various times considered related to land pulmonates or to opisthobranchs, but are now combined with the Rathousiidae and Onchidiidae to form the Soleolifera (Taylor and Sohl, 1962).

A small colony was obtained by Dr. John Burch near Tallahassee, Florida, and bred at the author's laboratory for several years. The slugs were maintained in plastic containers and were fed with lettuce, calcium carbonate, and a mixture of protein/mineral semi-synthetic diet sprinkled as powder onto filter paper or paper towel. Freshly laid and incubated eggs were examined by dissecting microscope or polarizing microscope, and some were embedded in paraffin or plastic (Paraplast) for sectioning after fixation in 10% formalin or 2% glutaraldehyde. The calcium content of fresh intact eggs and other tissues was measured by dissolving the material in a solution of 5% HCl (v/v) in 1%  $\text{La}_2\text{O}_3$  (w/v) in deionized distilled water and diluting serially, followed by analysis for calcium with a Perkin-Elmer Model 272 atomic absorption spectrophotometer. Analyses were done in triplicate. The lanthanum solution is used to eliminate interference by aluminum, sulphate and phosphate.

The animals were kept on a general 12/12 hour lighting period; ovipositing slugs were usually seen in late afternoon or early evening under these conditions.

#### RESULTS

The slugs are shiny, velvety black, about 4 cm or longer under normal inactive conditions; they can stretch much longer during locomotion. Once oviposition commences, the slug assumes a coiled position, so that its anterior and posterior ends slightly overlap. Eggs are released individually at an average of 45 minutes per egg until the entire clutch is formed. During laying, the slug moves slowly in a clockwise direction as viewed dorsally, so that the eggs



become wound into a clockwise coil; the entire egg mass is either one or two tiers thick, forming a disc-shaped object (Plate 5, fig. 1). One of the most striking characteristics of the clutch is that the last egg is attached to a long strand of mucus, often 6 cm long, which is then wound around the outer periphery of the egg mass, holding it together. This mucus strand is 1 or 2 mm thick and is the extension of a mucus rope which connects all the eggs. Each egg measures about  $8 \times 4 \times 4$  mm, and a single clutch ranges from 3-15 eggs.

The entire clutch is yellowish and quite transparent; the mucus strand is so sturdy that if one egg is picked up, the others all come with it, and individual eggs are dissociated only by some effort. Thus, this clutch is totally different from the individually deposited eggs of some land pulmonate snails. The entire egg mass is speckled with thin brown, green or yellow coloured coiled strands which on closer examination prove to be of faecal origin. The colour is determined by the diet of the animal. Each individual egg is directly invested by such faecal material (see Plate 5, fig. 2).

Perhaps the most significant observation in this study is the discovery of calcium carbonate spherules on the outer coat of each egg (Plate 5, figs. 3-4). These structures were overlooked even in this laboratory for quite some time because 1) there are only a few, very small calcium carbonate spherules on each egg, 2) although they were often birefringent under crossed polarizers, they occasionally appeared to be amorphous (*i.e.*, non-crystalline) and finally, 3) these spherules decrease in number and may disappear as the embryo inside develops.

Other basic information about the eggs of *Veronicella ameghini* is given in Table 1, including wet and dry weights per egg, calcium content per egg, wet weight of adults, and the range of eggs per clutch. Time of development is 20 days at normal room temperature in this laboratory (20°C).

Calculations from the data presented in Table 1 show that while the embryo of *Veronicella* has 30 µg of calcium by the time of hatching, only about 20% of this can come from the albumen fluid as a source; for the rest of this, the egg shell calcium stores must have been utilized.

\*TABLE I

|                                |                                            |
|--------------------------------|--------------------------------------------|
| Dimensions of eggs             | $8.54 \pm 0.82$ by $3.95 \pm 0.07$ mm (10) |
| Wet weight eggs                | $76.3 \pm 4.7$ mg (10)                     |
| Dry weight eggs                | $4.5 \pm 0.4$ mg (4)                       |
| Calcium content per egg        | $33 \pm 3.0$ µg (7)                        |
| Calcium content of egg albumen | $7.6 \pm 0.8$ µg (4) = 3.8 mMolar          |
| Volume of egg albumen          | 50 µl approximately (10)                   |
| Number of eggs per clutch      | 5 (= mode), range 3-15 (20)                |
| Wet weight of mature adults    | $1.45 \pm 0.10$ gm (4)                     |
| Calcium content of neonate     | $34.6 \pm 7.0$ µg (10)                     |

\* Figures are given as mean  $\pm$  standard deviation, with sample size in parentheses.

## DISCUSSION

I. *Veronicella*. The ultimate origin of the calcium carbonate spherules in *Veronicella* eggs is not known and will be investigated in future studies. Because these deposits disappear during development just as calcite deposits disappear in partly calcified eggs (Tompa, 1974) and heavily calcified eggs of pulmonates (Tompa, 1975), it seems that *Veronicella* also uses egg shell calcium for embryonic needs during development. This animal is a slug and has no shell, but slug bodies do usually contain large amounts of tissue calcium in the digestive gland, connective tissue cells and dermis (unpublished observations), and mucus stabilization is known to require calcium.



II. *Sources of calcium for the aquatic eggs of freshwater and marine molluscs.* The limited information which exists regarding the dependence of aquatic eggs on obtaining calcium from surrounding waters—fresh or marine—suggests that molluscan eggs laid in water do indeed concentrate certain ions during development. For freshwater pulmonates, *i.e.*, *Physa*, Lunetta (1971) made the general claim that the egg jelly ('mucin') contains calcium which is utilized by the developing embryos; snails deprived of this egg jelly were claimed to hatch with reduced shells, though no experimental protocol, techniques or data were given to support this very general statement. Needham (1942) discussed this topic and stated that the works of Block and Burdorch suggest that eggs of *Lymnaea stagnalis* (L.) contain more ash at hatching than at time of deposition. The studies by Taylor (1973) on *Lymnaea stagnalis* eggs show that the egg fluid is a dynamic physiological buffer for ions; this is consistent with the idea that there is a general dependence of such eggs on a minimum water calcium concentration below which the embryos turn opaque and die.

The status of marine molluscan eggs is somewhat better documented. Walls of the egg capsules of *Urosalpinx cinerea* Say are permeable to a wide variety of agents, including inorganic material (cited by Pechenik, 1978). Needham (1942) reviewed the literature and noted that in eggs of the marine gastropod *Volema (Hemifusus) tuba* Gmelin, an intake of Ca, Mg, SO<sub>4</sub>, Cl, and to a lesser extent Cu and F occurs. More careful and complete work has been performed with the ash-balance of cephalopod eggs, as reviewed by Needham (1942). In the squid *Sepia officinalis* L., the weight of the entire egg rises during development from 75 mg to about 135 mg. Much of the increase is accounted for by the intake of water, but the total egg ash actually rises from less than 1 mg to about 3.5 mg, showing that this cephalopod egg is dependent on sea water salts. As a matter of fact, the squid embryo not only concentrates calcium (eighty fold!) but also accumulates Na, K, Mg, P, and the less abundant ions of Cu, Fe, Mn, Mo, V, B, Li, Ni, Si, Sr, Ti and Zn from sea-water. These results for *Sepia* have been confirmed for several species of the squid *Loligo* (Needham, 1942). Cephalopod eggs and marine gastropod eggs, therefore, are not provided with sufficient calcium or water or many metals for development and hatching.

III. *Occurrence of calcium in other terrestrial gastropod eggs.* Land snails are generally placed into several major groups, though each of these may be polyphyletic in turn. The following arrangement is convenient for the present discussion: 1) land pulmonates, 2) the Soleolifera, 3) archeogastropod prosobranchs (Neritacea) and 4) mesogastropod prosobranchs. The pulmonates are by far the most successful both in terms of range of distribution and diversity. There are over 15,000 species found from the tropics to as far north as Iceland and Greenland. The other three groups are limited to tropical and subtropical zones, and comprise only about 5,000–6,000 species. I have listed in Table II the families of gastropods known to have (at least some) terrestrial members; to my knowledge this is the most comprehensive list of its kind. In a few cases there may be disagreement about whether individuals are terrestrial, amphibious or just supratidal, but it serves the point of showing which groups should be examined for terrestrially deposited eggs in future studies.

Among land pulmonates, more than 36 families are known to lay eggs with large provisions of calcium in the form of calcite crystals (Tompa, 1976). Families considered most ancient, such as the Partulidae and other orthurethrans, as well as the Endodontidae, Zonitidae, etc. are all characterized by having a thick shell of calcium carbonate around the egg (Tompa, 1976). Not all Stylommatophora are oviparous, for many retain the eggs or are ovoviviparous (Tompa, 1979a, b) and in general, these eggs are also calcium covered.

The closest relatives of the successful land pulmonates are the freshwater pulmonates, the Basommatophora. As far as I know, not a single species of Basommatophora has calcium deposits around its eggs. Except for a few volutids which have calcium particles on egg capsules (Morton, 1967; Ponder, 1970) and some Neritidae (discussed below), none of the marine gastropods elaborates calcium.

The polyphyletic origin of land snails is reflected in the various ways in which they coat their



eggs with calcium. In land pulmonates, calcium is mobilized from stores in the body (either shell and/or digestive gland), in the *ionic form*, so that total blood calcium content is greatly increased – by 60% – during egg shell calcification (Tompkins and Wilbur, 1977). Transport across the uterine wall is accomplished by a very specialized cell type. This calcium crystallizes into calcite only after ionic calcium is concentrated on the egg surface, inside the uterus.

The family Neritidae has marine, freshwater and terrestrial members and many are amphibious. In this group, it has been found that some animals have a specialized sac in the reproductive tract of the female (they are dioecious) which stores calcium carbonate spherules. When egg capsules are formed, these concretions move unchanged and coat the upper portion of each capsule. The original source of the spherules is the digestive gland, and interestingly, these spherules appear to be species specific in morphology (Andrews, 1937). Other members of this family have the so-called reinforcement sac but lack spherules; these species use diatoms and other ooze that they have ingested to coat their egg capsules. The important question of the exact relationship between terrestrial oviposition and use of calcium carbonate spherules is not yet fully answered in this family, but the terrestrial *Nerita birmanica* Phil. lives in mangrove swamps and deposits its eggs on trees, on snail shells, and on firm soil; these egg capsules have a calcified covering (Berry *et al.*, 1973).

Most fascinating is the independently evolved method of egg calcification found in the mesogastropod *Cochlostoma septemspirale* (Razoumowski), family Cochlostomatidae. This snail ingests large amounts of chalk forming chalky faecal pellets. At egg laying, the adult holds each egg by the foot while using its mouth to transfer and fix the calcium-rich faecal pellets to the surface of each egg (Prince, 1967). The amount of calcium possibly contributed by the reproductive tract is not known. This snail is known to be a strict calcicole, *i.e.*, found only in soil of very high calcium content.

Some other gastropods, namely *Pomacea* and *Pila*, of the family Ampullariidae, are aquatic or amphibious around freshwater, but they lay their eggs completely out of water. This is not unusual in freshwater snails. Each egg is released individually by the female and is studded with calcium carbonate spherules (Hall and Taylor, 1971). The eggs are soft when released, but adhere to each other and harden soon after exposure to air, finally resembling a praying mantis cocoon. The ultimate source of these spherules is the digestive gland. In *Pila*, at least, these spherules are then kept in the vaginal sac until egg laying (Meenakshi, 1955). Each egg is mechanically coated by a layer of pre-formed calcium carbonate spherules inside the snail. Whether ionic calcium is also transported across the uterus to the egg surface at the same time is not known. In *Pomacea paludosa* (Say), the situation is slightly different in that the spherules are most abundant in the albumen gland itself, not in the capsule gland nor in the vagina (Meenakshi *et al.*, 1974). The mineralogical form of the spherules in both of these genera is the unstable and unusual polymorph of calcium carbonate, vaterite (see also Hall and Taylor, 1971). The significance of having vaterite instead of calcite in a biological system is not understood. Ampullariid snails which lay calcified eggs differ from all other groups with similar eggs in one fundamental respect. Ampullariids such as *Pomacea* lay their eggs above water in order to escape aquatic predation of eggs; they do not have any other part of their life cycle taking place terrestrially. The aposematic red coloration of some of these egg masses (Snyder and Snyder, 1971) further suggests plasticity in response to aquatic predation rather than a general tendency towards evolution of a fully terrestrial life.

Why should the occurrence of  $\text{CaCO}_3$  deposits be correlated with terrestrial eggs and if this relationship is really significant, how do other terrestrial snails manage?

In the first case, egg shell calcium is necessary for the formation of the embryonic shell of land pulmonates; these eggs do not store enough calcium in the albumen to allow shell formation by the time of hatching (Tompkins, 1974, 1975). As a matter of fact, most land snail neonates seen in this laboratory also eat all of the egg shell (calcium) which is left after hatching. A similar embryonic utilization of egg shell calcium during development was later shown to



occur in the eggs of *Pomacea*, the only aquatic prosobranch which lays its eggs out of the water (Meenakshi and Watabe, 1977). The present study shows the same phenomenon for the soleoliferan *Veronicella ameghini*. The pattern seems clear – embryos need more calcium than can be provided in the egg albumen. Why can't the albumen hold more calcium? It is possible that higher calcium concentrations (*i.e.*, soluble calcium) would denature or salt-out some proteins, and/or would make it difficult for the embryonic cells to regulate their intracellular calcium concentration. Animal cells are generally known to be around  $10^{-6}$  molar in calcium in the cytoplasm, and this is maintained by a constant outward pumping of calcium by cells; higher intracellular calcium is toxic (Simkiss, 1967). A survey of the calcium content of avian and some reptilian egg albumens is consistent with the idea of (having to keep) low albumen calcium levels (see data of Simkiss, 1967).

How do other terrestrial snails provide calcium to their embryos? Many terrestrial or amphibious prosobranchs, such as *Pomatias*, are known to cover their terrestrial eggs with soil (Creek, 1951). The reason for this is here proposed to be the following: the soil of their habitat is known to be rich in lime, *i.e.*, calcium carbonate, and by attaching soil to the egg surface, an intimate contact is made between the egg and this calcium source. (If, instead, eggs were just laid inside a pocket of soil, especially when a large clutch were involved, most of the eggs would not be in direct contact with the soil calcium.) This reasoning would also explain why an animal such as *Pomatias elegans* (Müller) releases only one egg at a time, in order to coat each one with soil (calcium). Creek (1951) mentions that the ecological needs of *Pomatias elegans* include 'a thin layer of comparatively alkaline soil (pH 7.7–7.9) . . . (which) covers calcareous rocks.' Further support for this line of reasoning is Creek's other observation (1951, p. 633) that:

'The embryo will not develop either in distilled or tap water, but only in water which has been shaken with, or is in contact with, soil, so that it is a relatively concentrated solution of soil salts.'

I have no doubt that the 'salt' which will be found essential is calcium, although Creek (1951) calls it an 'unknown factor'.

This line of reasoning may also turn out to be fruitful in explaining why the eggs of *Pomatiopsis lapidaria* (Say), described by Dundee (1957), are also laid in the soil by this aquatic prosobranch living so close to the shore of streams, and why again, each egg is completely covered by a tightly applied layer of soil, the 'husk'. In the amphibious *Oncomelania quadrasi* Moellendorff the eggs are similarly covered by agglutinated sand, soil, or mud, as revealed by Abbot (1946).

For the many other groups of terrestrial gastropods (see Table II) it appears that we just don't have any information, as bemoaned by Spence (1939) and others.

To postulate a new evolutionary role for an organ (preadaptation), one should find that at a given time two organs perform the same (overlapping) functions and that at least one of these organs performs two functions. With some of the preceding examples the two organs involved would be 1) the rectum, passing out calcium-rich faecal pellets of the surrounding soil, as with *Cochlostoma septemspirale* today, and 2) the capsule gland or uterine gland, which provides the surface mucus cover of the egg itself, the egg shell. It is the rectum which has the two-fold function of excretion as well as calcium provision, while certain cells of the capsule gland, normally charged with elaborating some mucopolysaccharide egg covering, gradually evolve into cells specialized for providing more calcium across their walls. This cation is then bound by the mucopolysaccharide/protein surface's negative charges.

Calcium rich soils are but a subset of the vast array of terrestrial habitats and it is only in these areas that faecal pellets composed of soil provide enough calcium for embryonic development. It therefore follows that in other habitats selection would favour variation in snails which use other sources of calcium, or at least which can temporarily store calcium in some mode. When oviposition occurs in marginal habitats, those animals which provide more calcium directly into the egg shell – as opposed to relying only on faecal pellets or merely coating



the egg surface with soil particles – have greater success. The case examined in this study, that of *Veronicella ameghini*, resembles this intermediate stage of development, where not only faecal calcium, but stored calcium in the form of cellular spherules, are incorporated onto the egg surface. The development of a second form of (stored) calcium provision opened new ecological areas and niches for colonization, i.e. areas of land which have, say, less than 6% soil calcium, which is the limiting factor for the distribution of *Pomatias elegans* in England today (Fretter and Graham, 1962).

TABLE II

Families of gastropods known to include terrestrial species (compiled from numerous sources).

## CLASS GASTROPODA

|                           |                            |
|---------------------------|----------------------------|
| subclass Streptoneura     | superfamily Rissoacea      |
| order Archeogastropoda    | Hydrobiidae                |
| superfamily Neritacea     | Truncatellidae             |
| Neritidae                 | Assimineidae               |
| Helicinidae               | Aciculidae                 |
| Hydrocenidae              | Vitrinellidae              |
| order Mesogastropoda      | order Basommatophora       |
| superfamily Cyclophoracea | superfamily Ellobiacea     |
| Cyclophoridae             | Ellobiidae                 |
| Maizaniidae               | order Stylommatophora      |
| Poteriidae                | all                        |
| Pupinidae                 | order Soleolifera          |
| Cochlostomatidae          | superfamily Veronicellacea |
| superfamily Littorinacea  | Veronicellidae             |
| Pomatiidae                | Rathousiidae               |
| Chondropomidae            |                            |

This theory does not require that the proto-terrestrial animals fed on soil or ooze at all times; they probably regularly fed on vegetable matter or fungal hyphae. But at the critical time of egg laying, calcium must always be accessible in their immediate environment. As a matter of fact, reproductive use of intestinal calcium may occur even in the most advanced pulmonates of today concurrently with mobilization from stored digestive gland or shell deposits, *but via the blood*, while the eggs are still inside the reproductive tract. In a similar light, although female birds use a special medullary bone for egg shell formation to a considerable extent, if a large amount of intestinal calcium is available, this is also readily absorbed for egg shell formation, again *via the blood* (see Simkiss, 1967). What is common to both cases is that they are not restricted to exclusive use of calcium from intestinal contents at the time of egg shell formation.

One more serious question needs to be examined: once land snails have evolved the calcified egg shell covering, though they occupy a new variety of niches, they are still limited by the need to obtain a lot of calcium periodically. Have they 'followed up' the possibility of obviating this calcium dependence by becoming shell-less and simply forgoing or modifying calcium dependent functions and structures? The answer turns out to be a qualified yes. An examination of the list by Tompa (1976) shows that at least five slug families have some species forming calcified eggs: Arionidae, Philomycidae, Parmacellidae, Milacidae and Limacidae. The known eggs of these slugs usually have a very reduced amount of calcite crystals on their surface and are not hard-shelled; many of these slugs in fact have no trace of crystals, though chemical analysis indicates that calcium is still bound to the organic (mucus/protein) egg shell. (The slug-like animal, *Testacella* sp., which has only a minute, vestigial shell, forms eggs with a thick, hard, calcium carbonate shell. This, however, turn out to be a special case, since *Testacella* specializes in eating earthworms and has apparently evolved the slug habit for subterranean locomotion after its prey. Earthworms found in the ranges of *Testacella* are notoriously rich in calcium (from



eating the soil in their diet) and actually have calciferous glands which function to eliminate calcium. This highly specialized slug's food is unusually rich in calcium.) Land slugs have generally decreased their need for and dependence on egg calcium, but eggs must still be supplied with some amounts of this cation for use during embryonic development. An example of the importance of calcium even in the lives of slugs is the observation that the North American slug *Ariolimax columbianus* (Gould) has a small, calcified internal shell which is totally resorbed during egg laying, leaving only its organic matrix 'ghost'. Then the slug feeds and restores the calcium carbonate of its internal shell before ovipositing again (Meenakshi and Scheer, 1970). The semi-slug, *Vitrizonites*, also resorbs its reduced external shell during egg laying, so much so that its post-laying shell remnant looks 'wrinkled' (Tompa, 1974). But many slugs which have no shell remnant inside or outside still store large amounts of calcium in their soft tissues and some even lay eggs with calcite crystals e.g. *Philomycus carolinianus* (Bosc). Conversely, some slugs with internal shells lay eggs which have only organically bound calcium – considerable amounts still – in the egg cover, e.g. *Limax maximus* L. (Tompa, unpublished). And of course, the soleoliferan slug described in this paper has no shell but lays eggs with a covering of calcium spherules as well as faecal calcium. Therefore, on the basis of cases examined so far, slugs appear to have decreased the amount of the calcium in their eggs, even to the point where no crystals of calcium carbonate are seen, but they have not eliminated the need for a critical minimum amount for embryonic development.

I do not intend to suggest that provision of adequate calcium within the terrestrial egg is the only consideration in the evolution of successful land snails. No doubt, solutions to problems of desiccation and to changing nitrogen excretion from the urea or ammonia of aquatic forms to insoluble uric acid (uricotelic) are just two examples of other areas critical to the development of gastropod embryos in completely terrestrial eggs. I also recognize that each stage of a life cycle must be adaptive to the respective surroundings of the organism, from egg to adult. In fact, it is for this very reason that the source of embryonic calcium is here examined, for it is an important adaptive response to complete the transition to terrestrial life, a subject which has been neglected.

Calcium, of course, is not the only element supplied to the eggs of land snails: eggs of the pulmonate land snail *Anguispira alternata* (Say) were found to have the following elements within the egg albumen when examined by neutron activation analysis: Cl, Cr, Al, Mn, Mg, Zn, Zr, Si, V and Na; many other elements are surely also present here but were not detected because of the limitations of the specific technique and protocol used (Tompa, unpublished). It is not surprising, therefore, that when such eggs are deposited on ash-free filter paper and are kept at high humidity with de-ionized water, that these eggs develop normally and give rise to healthy young; the same has been observed for the eggs of the land pulmonate *Strophocheilus oblongus* (Becquaert) from Brazil (Tompa, unpublished). Because such eggs do not gain water during development, but can actually afford to lose considerable amounts, with the only 'outside' material needed for development being oxygen from the air, then such eggs of land pulmonate snails fulfill Needham's (1942) criteria for being called a cleidoic egg. Presumably many, though not all, of the other types of land snail eggs will be found to be similar upon examination.

#### SUMMARY

1. Among the polyphyletically evolved land snails, many different methods of egg shell formation are seen; what they all have in common is the provision, or storage, of large amounts of calcium in the egg shell for use during embryonic development.
2. Eggs of the terrestrial soleoliferan slug *Veronicella ameghini* have two sources of calcium for the developing embryo: 1) a thin, outer layer of calcium carbonate spherules, and 2) faecal material incorporated onto the egg shell surface. The egg albumen also contains calcium and may be



considered a third calcium compartment; but this amount is grossly insufficient to account for the amount of calcium found in the newly hatched embryo.

3. During *Veronicella*'s development, the calcium carbonate spherules dissolve and disappear; this is similar to previous observations made on eggs of certain land pulmonates.

4. The most simple form of calcium provision among the many types of terrestrial gastropods is that of covering the egg shell surface with soil particles rich in lime. Slightly more complex is the use of faecal pellets containing calcium-rich soil to cover each egg surface. All these snails are limited to soils very high in calcium.

5. A more commonly encountered method of storage of calcium occurs from intracellular calcium carbonate spherules, usually synthesized in the digestive gland. These spherules may eventually be transported to and stored in some diverticulum of the reproductive tract.

6. Successful land pulmonate snails are known to be able to use their shell (and possibly digestive gland stores) as a source of calcium during oviposition. Calcium carbonate is dissolved, transported *via* the blood in the ionic form, finally going across the uterine epithelium, and becoming re-precipitated on the egg shell matrix.

7. When laid in water, the eggs of both freshwater and marine molluscs obtain necessary elements, such as calcium, from the surrounding water. But even aquatic molluscs provide large amounts of calcium in the egg covering, however, if eggs are laid above the water or spray level.

8. Successful permanent invasion of terrestrial habitats apparently necessitates some method of providing calcium to the gastropod embryo in very large amounts, presumably for forming the embryonic shell, for mucus formation and other functions. Egg albumen seems incapable of maintaining the necessary concentration of this vital cation without harm to the embryo.

9. Even pulmonate slugs—which have greatly lessened their degree of dependence on calcium—provide their eggs with a significant amount of this cation in the egg shell, though this shell is often reduced to having only organically bound calcium, not crystals.

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## PLATE 5 (opposite)

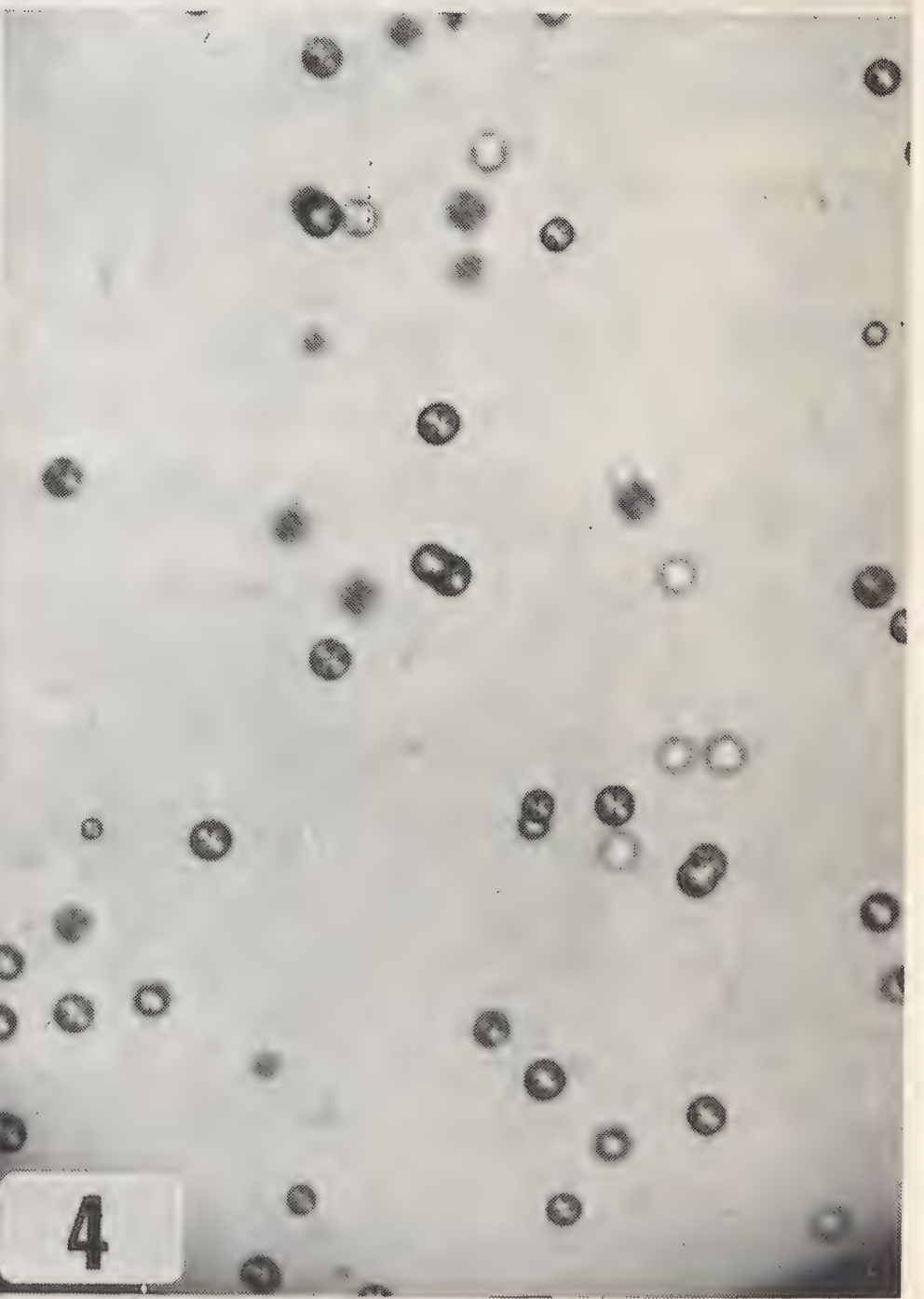
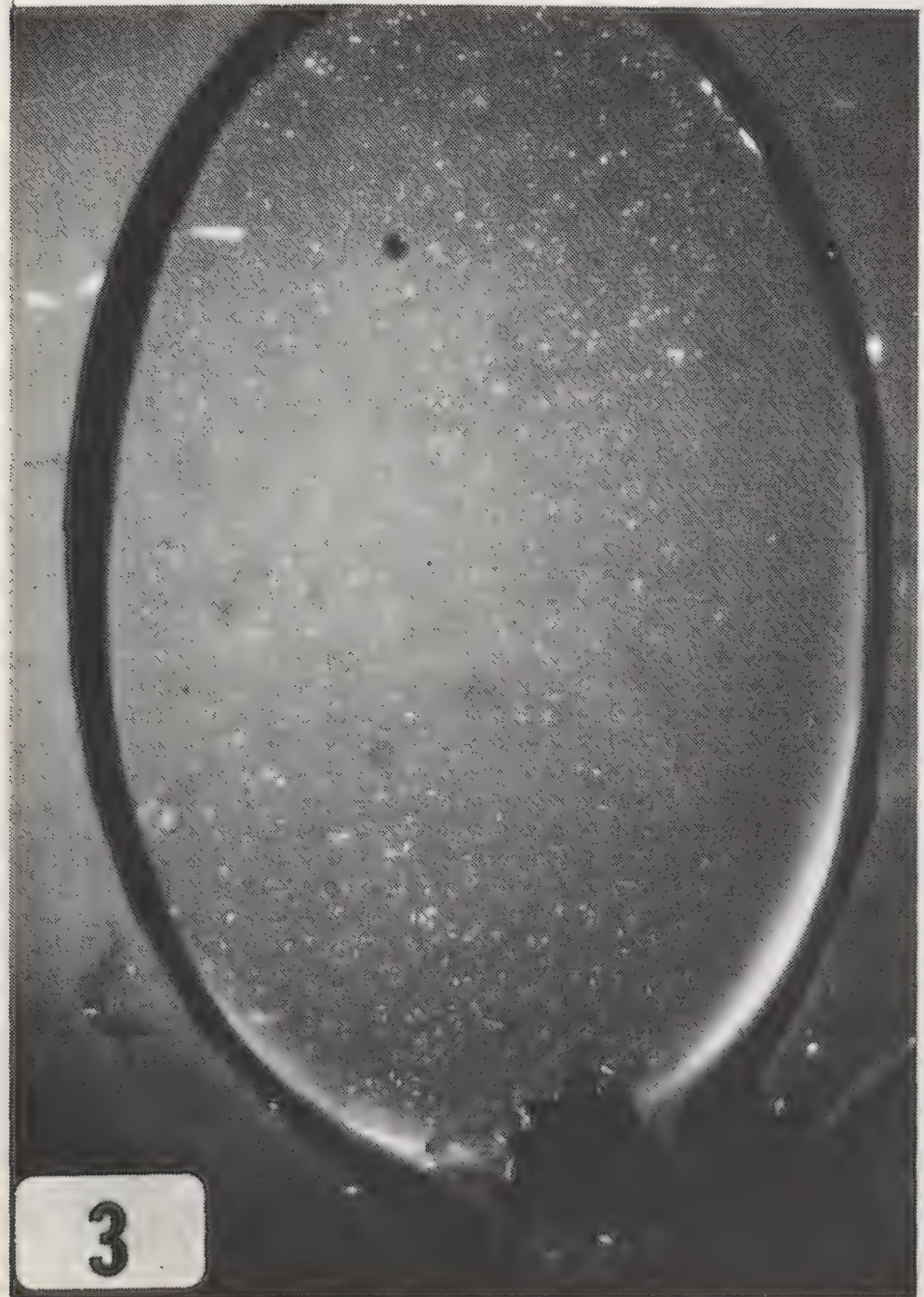
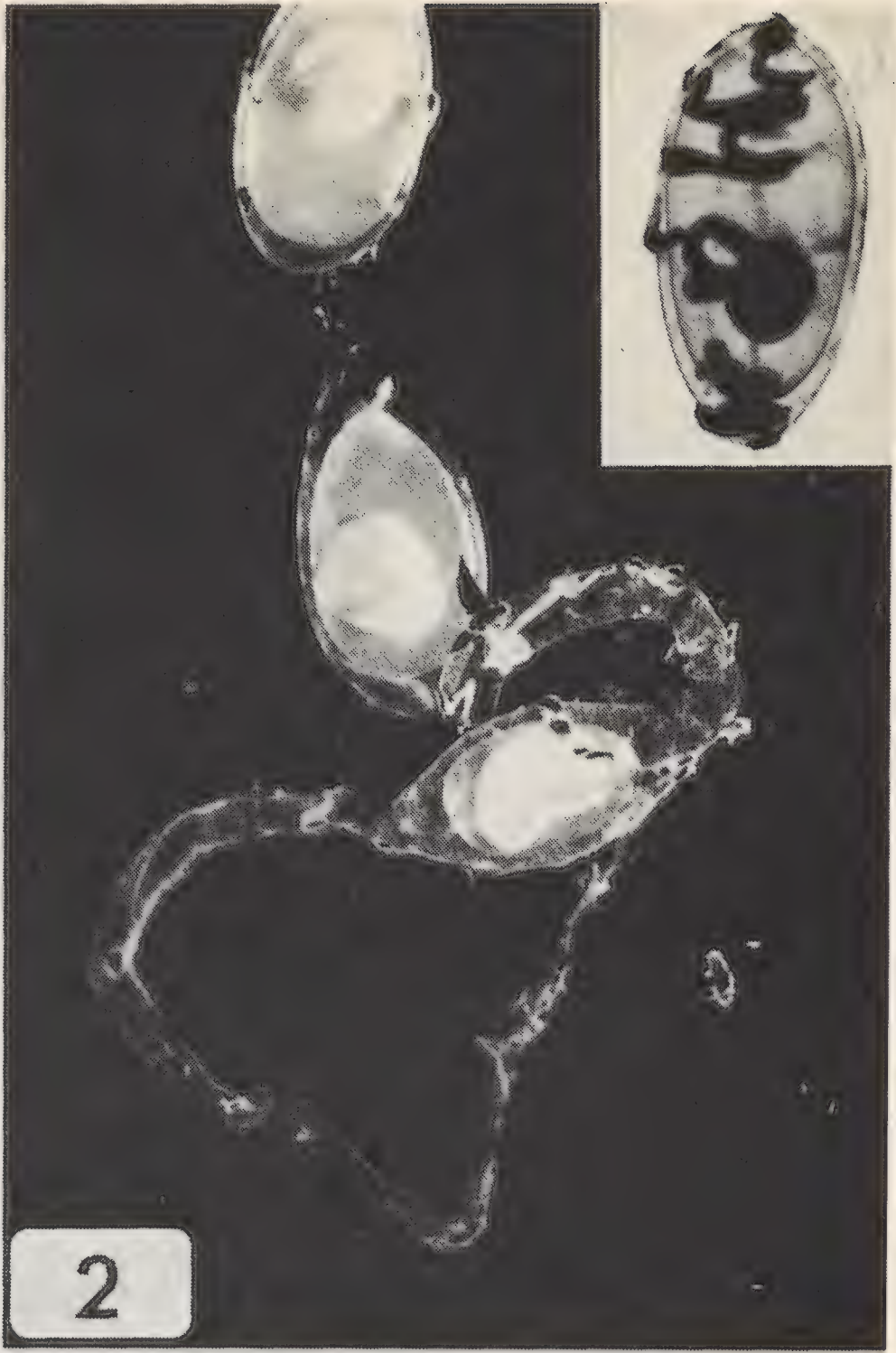
Fig. 1. *Veronicella ameghini* clutch upon completion. Each egg is approximately 8 × 4 mm and there are 6 eggs in this clutch which is peripherally surrounded by a mucus string. × 2.

Fig. 2. The spawn mass unravelled from its normal, coiled position, showing the strikingly large and thick mucus string connecting the eggs. × 4. Inset in upper right corner shows the closely applied faecal matter. × 5.

Fig. 3. Higher magnification of an intact egg, taken in a microscope under partially crossed polarizers. The egg shell surface or jelly surface is studded with numerous crystalline (i.e., birefringent) spherules. × 17.

Fig. 4. Higher magnification of the surface of a freshly deposited egg, viewed under partially crossed polarizers. The spherules are usually single, and have a maltese cross pattern under these circumstances; in several places fusion of two spherules can be seen clearly. × 130.











# THE LAND AND FRESHWATER MOLLUSCA OF ST. IVES, CORNWALL PART I: SHELL-BEARING SPECIES

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(Read before the Society, 15 December, 1979)

*Abstract:* A marked diversity of habitat type occurs within a small area on the northern coastal belt of Cornwall. The distribution of 43 species of land and freshwater molluscs is mapped on one-km square grid maps and their habitat frequency tabulated.

This survey includes all the land and freshwater molluscs found in the district of St. Ives, Cornwall (figs. 1 and 2), with the exception of the families Arionidae, Milacidae, Limacidae and Testacellidae.

The relative abundance and local ecological distribution of each species is shown in Table 1; while the localities in which they occur are plotted on a series of one-km square maps. The results were obtained during four years' field work between 1975-78.

## METHODS

During a period of four years from 1975-78, an area of approximately 32 km<sup>2</sup> was investigated to ascertain the type and distribution of the molluscan fauna it contained.

Each one-km square within the district was comprehensively searched. As far as was practical, all the squares were searched with equal thoroughness and habitats were explored irrespective of whether or not they appeared likely to contain molluscs. Confirmation that snails were absent from obviously poor habitats was regarded as being of equal importance to amassing positive records from richer sites. To this end large tracts of moorland, for example, were examined.

Field work was carried on throughout the twelve-month period of each year, and many localities were searched several times at different seasons. This method frequently added records to a square and ensured that species undetected on earlier visits were included. The most obvious example for which this technique proved necessary, was in the winter recording of *Vitrina pellucida* (Müller) whose presence is often impossible to detect in the summer months, but the range of other species was also extended by employing this continuous method.

All the records shown on the distribution maps relate to living specimens. Whenever dead shells alone were encountered further investigation was carried out to confirm that live animals were present. In the absence of living material the record was omitted from the maps. The number of squares in which only dead shells of a particular species could be found was small, and has not affected the overall pattern of distribution.



## THE AREA SURVEYED

The area covered by this survey is environmentally characteristic of the SW of Cornwall and also much of the northern and southern coastal areas in the county. A large proportion of the land and freshwater molluscs found in vice-counties 1 and 2 is present, and the habitat/species data presented in Table 1 are broadly representative of the county as a whole.

The district has a well-defined topographical zoning, divided into three components. Stretching along most of the southern border is a background of high acid moorland, with a north facing slope; descending from it is a flat belt of agricultural land, approximately  $1\frac{1}{2}$  km wide, aligned east to west, and below this the farmland is abruptly terminated by exposed steep cliffs. In effect these zones, moorland, farmland and sea cliffs, mark distinct habitats for some molluscs, the fauna being determined by the relative acidity and the extent and type of vegetative cover present. The urban areas of St. Ives and the range of sand dunes at Lelant, although small in extent, add further diversity to the overall habitat pattern.

The Land's End Peninsula is the most south-westerly point in the British Isles. It covers an area of about 83 km<sup>2</sup>, and the district of St. Ives forms its most north-easterly corner. Geologically the area is dominated by a huge granite mass which lies centrally down its entire length. In many places this granite terminates in high sheer cliff faces, Land's End itself providing one of the most spectacular examples. However, all the cliffs lying within the St. Ives district consist of either a dark, hard greenstone, or the softer laminated Mylor Slate.

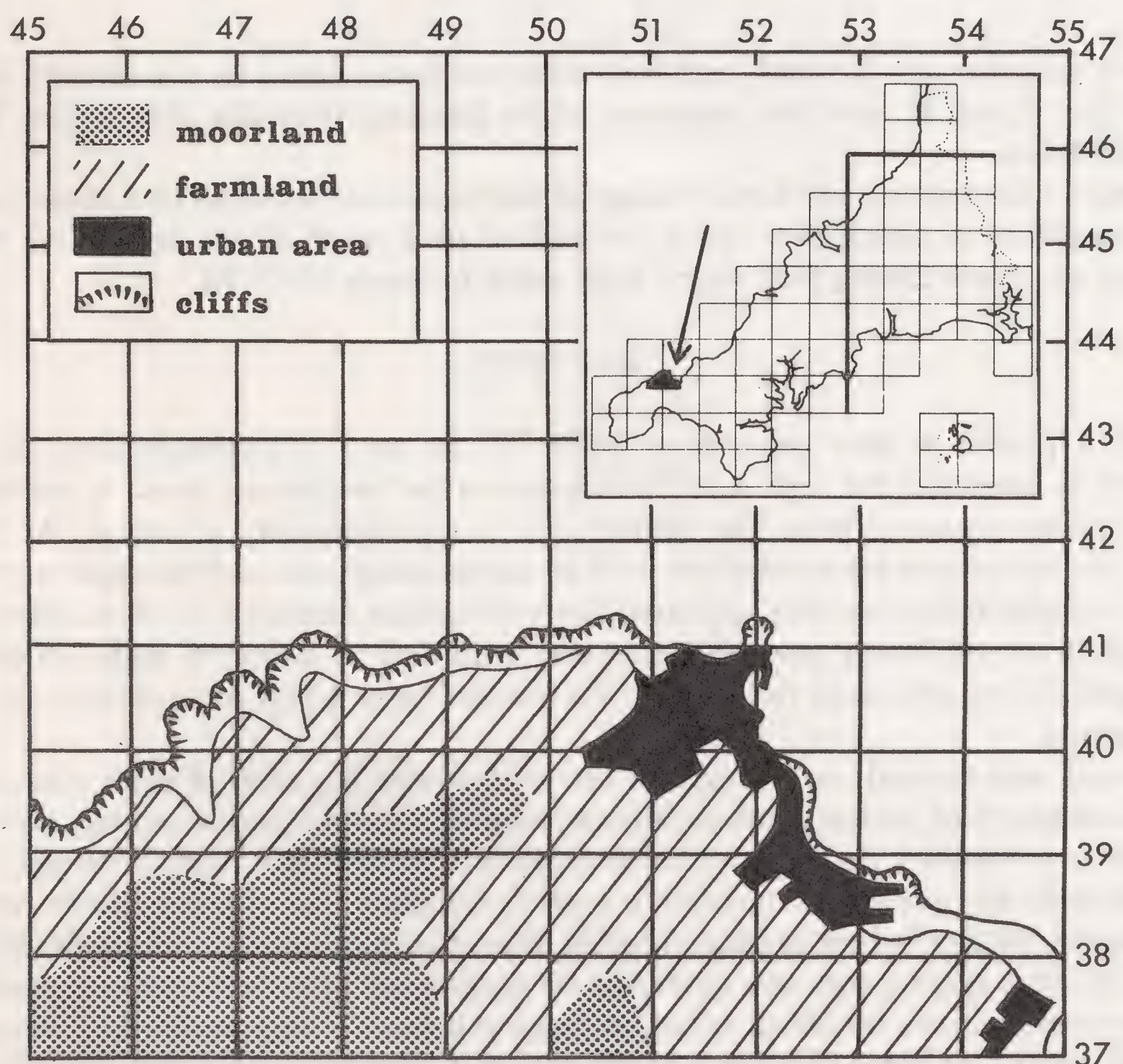


Fig. 1. St. Ives and district, showing the principal topographical zones. Insert: Cornwall, vice-counties 1 and 2, with the extent of the present survey indicated.



Inland, along the north coast, the land above the 150 m contour is characteristically exposed moorland, capped by granite carns, rising in places above the 240 m level. Stretching from St. Ives westwards and below the moorland, is a narrow, almost flat, platform of land, an ancient seabed possibly Pliocene in age, which slopes gently seaward between the 125 and 90 m contours. This marine shelf is now almost entirely given over to farmland, parts of which are still enclosed by the remnants of small irregular Iron Age field systems. Nearer to the coast the land curves over more rapidly, descending to 60 m before finally dropping away, down steep and rocky cliff faces. A number of narrow, deeply incised, valleys, usually overgrown with low dense scrub, or lightly wooded and with small swift streams flowing along their floors, cut through the platform of land at right angles to the coast.

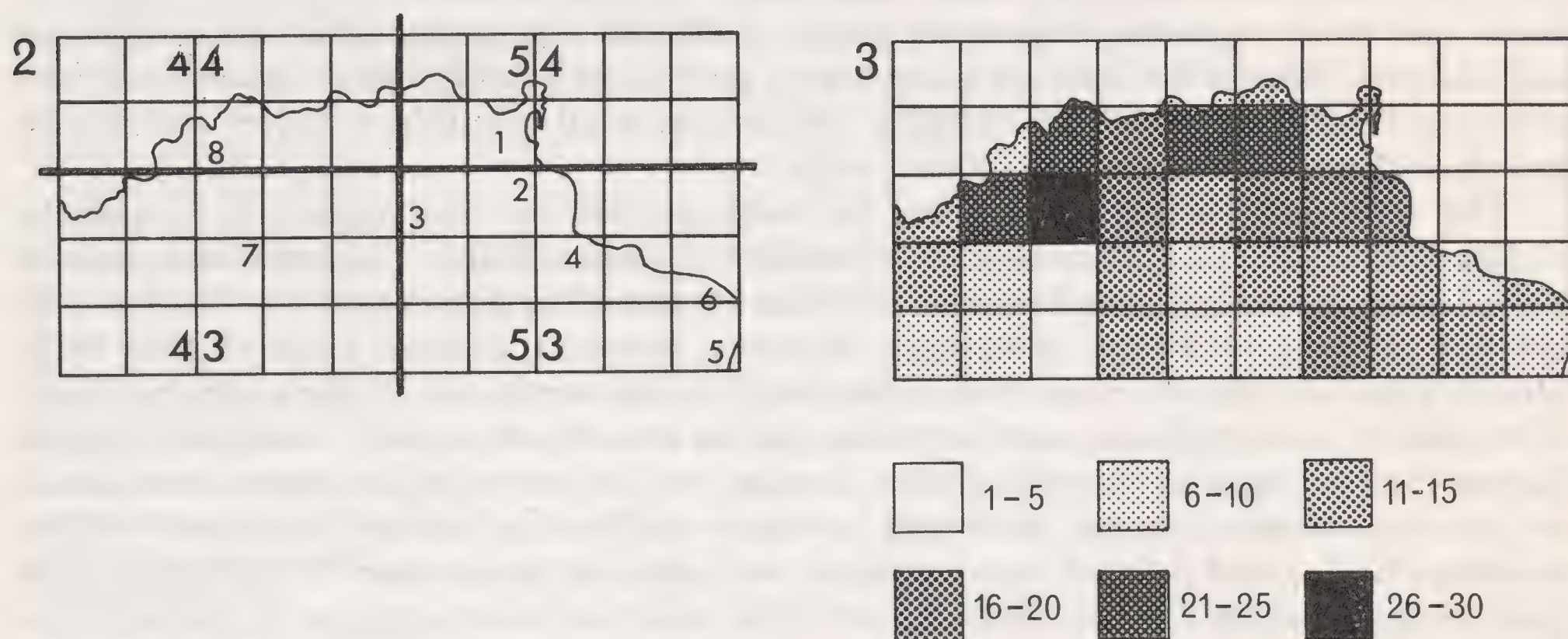


Fig. 2. The survey area showing both one-km and ten-km squares. Place names referred to in the text: 1 St. Ives. 2 Tregenna Wood. 3 Bussow Reservoir. 4 Carbis Bay. 5 Lelant. 6 Lelant golf course. 7 Trendrine Hill. 8 Treveal.

Fig. 3. Total number of species recorded in each 1 km square of the survey area.

Numerous small streams flow through the district, although the peninsula is too narrow for water courses of any significance to occur. High annual rainfall, together with poor drainage in many of the fields, contribute to the proliferation of marshy conditions in pastures, and to the frequency of more permanent marshes at the base of the moorland and on the cliff tops.

*Moorland.* Moorland covers almost one fifth of the area surveyed. It lies principally above the 150 m contour, and reaches a maximum of 243 m at the summit of Trendrine Hill. The thin layer of soil is dark, peaty and frequently waterlogged, although the sloping contours prevent the formation of bogs. Gorse (*Ulex* sp.) is common on the lower slopes, and areas of bracken (*Pteridium aquilinum* (L.) Kuhn) predominate on some of the more sheltered hillsides. Heathers and heaths (*Calluna vulgaris* (L.) Hull and *Erica* spp.) grow on the middle and higher ground. (Botanical nomenclature is that followed by Dandy, 1958; English names in Dony *et al.*, 1974) Strong winds sweep across the hills preventing the growth of any taller herbage, and the ground-cover at these altitudes consists entirely of various grasses, sedges and rushes.

Much of the moorland is devoid of molluscs. The species that do occur are almost always restricted to habitats near stone walls and their surrounding herbage, and among the debris of more recent mine workings. Old mine dumps frequently harbour species which have been introduced by human agency and which have persisted, such as *Helix aspersa* Müller. The shells of moorland snails often display signs of stunted growth, and adult specimens are commonly



smaller than those living only a short distance away in more congenial farmland habitats. The granite is never far below the surface on the moorland, and numerous outcrops of bare rock are visible. The area is highly acid and random soil-indicator colour tests gave results ranging between pH 4.50 and 5.25. However, isolated habitats more attractive to molluscs do occur in the vicinity of some of the old mine workings, with readings of pH 7. Artificial sites such as these provide a refuge for several species that would otherwise be alien to the moorland.

*Farmland.* The major area of farmland is restricted to the narrow 90 to 125 m marine platform, which runs along the northern edge of the district. The route followed by the present north coast road divides the moorland on one side from the farmland on the other, seaward, side. Generally the fields are small and irregular in shape, divided by traditional Cornish 'hedges' and less frequently by low stone walls built with loose unmortered granite. The Cornish 'hedges' are mostly of granite and other local rocks, constructed in double thickness and infilled with earth. Gorse and other vegetation commonly grows on the flat top, giving additional height and habitat cover. Most of the fields are given over to permanent grazing, often of poor quality due to encroaching bracken and waterlogging. In addition small quantities of barley and oats are grown, with some *Brassica* spp. and root crops.

The walls and 'hedges' surrounding the fields provide the most important habitats for molluscs on the farmland. Because of their inability to retain sufficient moisture over a period of time through the lack of vegetative cover, and also because of the disturbance from livestock, the pastures, as such, are devoid of molluscs. However, marshy conditions found in some fields, provide ideal habitats for certain *Pisidium* and other freshwater species. In the south-east corner of the district, between Lelant and Carbis Bay, lies an area of better quality farmland. The field patterns here are more in line with modern farming practice, extending over many acres. Snails are generally absent from the fields and are again confined to habitats associated with the boundary hedges and isolated copses. Colour tests taken on the northern belt of pastureland gave average readings of pH 6, the proximity of the moorland being apparent by the scarcity of neutral or alkaline conditions.

*Cliffs.* The cliff exposures consist of two types of rock: a very hard greenstone, and a weaker laminated Mylor Slate which is more easily dissected by the action of the sea. None of the cliffs rises above 60 m, and they are less spectacular in appearance than those lying to the east and west of St. Ives. Although some are almost vertical, many slope more gently seaward and are capped with turf and areas of bracken and low gorse bushes.

The exposed windswept aspect of these north-facing cliffs precludes large numbers of molluscs from inhabiting them. In addition they are slightly more acid than the pastures above, with average colour indicator readings of pH 5.25. The snails that do live here tend to be found in sheltered situations, on the lee side of walls and beneath stones. Extensive areas of bracken and exposed rock faces are almost devoid of molluscs. However, snails are frequent in the turf on the slopes of some promontories: *Cepaea nemoralis* (L.), *Helix aspersa* Müller and *Ponentina subvirescens* (Bellamy) are characteristic species.

*Sand dunes.* Lying to the south-east of the district is a narrow strip of sand dunes, part of the much larger range of dunes extending around the eastern perimeter of St. Ives Bay. They are rich in shell sand and support large colonies of xerophiles as well as molluscs of more generalized habitats. Lelant golf course, which is laid out on old dunes, provides a further extension of this habitat, although the number of snails found here is not so great. The dunes are stabilized by large areas of marram grass (*Ammophila arenaria* (L.) Link.). Behind the marram grass, turf and a typical dune flora consolidates the transition to the outlying golf course and pastures. The area is completely exposed to the northerly on-shore winds.

*Woodland.* Woodland and stands of trees are not a dominant feature in the landscape of west Cornwall. This is primarily due to the intensive grazing of cattle on the lower moors and pastures, and the exposed aspect of the area to the full force of the winter gales. The frequent salt-laden winds affect the district from all directions. Small stands of mixed trees are established



THE LAND AND FRESHWATER MOLLUSCA OF ST. IVES

TABLE 1

|                                            | A | B | C | D | E | F | G | H | I | J | K | L | M |
|--------------------------------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Terrestrial species:                       |   |   |   |   |   |   |   |   |   |   |   |   |   |
| <i>Carychium tridentatum</i> (Risso)       | — | r | — | — | c | — | — | — | — | — | — | — | — |
| <i>Oxyloma pfeifferi</i> (Rossmässler)     | — | — | — | — | — | — | — | — | — | o | — | o | — |
| <i>Cochlicopa lubrica</i> (Müller)         | r | c | o | c | c | c | — | — | — | — | — | — | — |
| <i>Cochlicopa lubricella</i> (Porro)       | — | o | o | c | c | o | — | — | — | — | — | — | — |
| <i>Lauria cylindracea</i> (Da Costa)       | — | c | o | c | o | o | o | o | o | — | — | — | — |
| <i>Acanthinula aculeata</i> (Müller)       | — | — | — | — | o | — | — | — | — | — | — | — | — |
| <i>Discus rotundatus</i> (Müller)          | o | c | c | c | c | c | o | — | o | — | — | — | — |
| <i>Vitrina pellucida</i> (Müller)          | r | c | c | c | c | c | o | — | — | — | — | — | — |
| <i>Vitrea crystallina</i> (Müller)         | — | — | — | — | c | o | — | — | — | — | — | — | — |
| <i>Vitrea contracta</i> (Westerlund)       | — | r | — | — | — | r | r | — | — | — | — | — | — |
| <i>Nesovitrea hammonis</i> (Strom)         | o | — | — | — | — | o | o | — | — | — | — | — | — |
| <i>Aegopinella nitidula</i> (Draparnaud)   | r | c | c | c | c | c | o | — | — | — | — | — | — |
| <i>Oxychilus draparnaudi</i> (Beck)        | — | c | o | — | o | — | — | c | — | — | — | — | — |
| <i>Oxychilus cellarius</i> (Müller)        | r | o | o | c | o | o | o | — | — | — | — | — | — |
| <i>Oxychilus alliarius</i> (Müller)        | o | c | o | c | c | c | o | — | — | — | — | — | — |
| <i>Oxychilus helveticus</i> (Blum)         | r | c | c | c | o | c | — | — | — | — | — | — | — |
| <i>Zonitoides excavatus</i> (Alder)        | o | — | — | — | — | o | — | — | — | — | — | — | — |
| <i>Euconulus fulvus</i> (Müller)           | — | — | — | — | — | o | o | — | — | — | — | — | — |
| <i>Clausilia bidentata</i> (Strom)         | o | c | c | c | c | c | c | c | — | — | — | — | — |
| <i>Balea perversa</i> (L.)                 | — | — | — | — | c | c | — | — | — | — | — | — | — |
| <i>Candidula intersecta</i> (Poiret)       | — | o | o | o | — | — | — | c | o | — | — | — | — |
| <i>Cerņuella virgata</i> (Da Costa)        | — | o | — | c | — | — | — | a | o | — | — | — | — |
| <i>Helicella itala</i> (L.)                | — | — | — | — | — | — | — | o | — | — | — | — | — |
| <i>Cochlicella acuta</i> (Müller)          | — | o | — | o | — | — | — | a | o | — | — | — | — |
| <i>Trichia striolata</i> (C. Pfeiffer)     | r | c | o | c | o | c | o | — | o | — | — | — | — |
| <i>Ashfordia granulata</i> (Alder)         | r | c | c | c | o | c | o | c | — | — | — | — | — |
| <i>Trichia hispida</i> (L.)                | r | c | c | c | o | c | o | r | — | — | — | — | — |
| <i>Ponentina subvirescens</i> (Bellamy)    | — | — | — | — | — | — | o | — | — | — | — | — | — |
| <i>Theba pisana</i> (Müller)               | — | — | — | — | — | — | r | — | — | — | — | — | — |
| <i>Cepaea nemoralis</i> (L.)               | o | c | c | c | o | o | c | a | — | — | — | — | — |
| <i>Cepaea hortensis</i> (Müller)           | — | o | o | o | — | — | r | — | — | — | — | — | — |
| <i>Helix aspersa</i> Müller                | o | c | c | c | o | o | c | c | a | — | — | — | — |
| Freshwater species:                        |   |   |   |   |   |   |   |   |   |   |   |   |   |
| <i>Potamopyrgus jenkinsi</i> (E. A. Smith) | — | — | — | — | — | — | — | — | — | c | a | c | — |
| <i>Lymnaea truncatula</i> (Müller)         | — | — | — | — | — | — | — | — | — | — | — | — | c |
| <i>Lymnaea glabra</i> (Müller)             | — | — | — | — | — | — | — | — | — | — | — | — | o |
| <i>Lymnaea peregra</i> (Müller)            | — | — | — | — | — | — | — | — | — | o | c | c | c |
| <i>Ancylus fluviatilis</i> Müller          | — | — | — | — | — | — | — | — | — | c | — | — | — |
| <i>Pisidium casertanum</i> (Poli)          | — | — | — | — | — | — | — | — | — | o | c | — | c |
| <i>Pisidium personatum</i> Malm            | — | — | — | — | — | — | — | — | — | c | c | — | c |
| <i>Pisidium obtusale</i> (Lamarck)         | — | — | — | — | — | — | — | — | — | o | — | — | — |
| <i>Pisidium milium</i> Held                | — | — | — | — | — | — | — | — | — | — | o | — | o |
| <i>Pisidium subtruncatum</i> Malm          | — | — | — | — | — | — | — | — | — | — | o | — | o |
| <i>Pisidium nitidum</i> Jenyns             | — | — | — | — | — | — | — | — | — | — | o | — | — |

Table 1. Habitat frequency of molluscs found live in the district. A moorland. B wasteland. C farmland. D Cornish 'hedges'. E woodland. F scrubland. G cliffs. H dunes. I cultivated gardens. J streams. K ponds and reservoir. L ditches. M marsh. a abundant. c common. o occasional. r rare.

in the outlying areas of St. Ives, mainly confined to the eastern and more sheltered side of the town. The most important from the point of view of molluscs, is a small woodland situated on the outskirts of the town, Tregenna Wood. Elm (*Ulmus* sp.) and sycamore (*Acer pseudoplatanus* L.) are the predominant trees, with some ash (*Fraxinus excelsior* L.) and pine (*Pinus* sp.) and introduced *Hydrangea* sp. provide a dense undergrowth in some parts of the wood. A somewhat larger wood of a similar type occurs at Lelant.

A further semi-wooded area lies to the west of St. Ives, on the steep sides of a narrow valley at



Treveal. Here scattered remnants of woodland merge with thick scrub. Willows (*Salix cinerea* L. subsp. *atrocinerea* (Brot.) Silva Sobrinho) are dominant, growing abundantly on the waterlogged floor of the valley. Sycamore is also present, and a grove of wind stunted elms is established on an east facing slope. The diverse range of habitats contained in this relatively small area, results in the valley being particularly rich in molluscs; almost 75% of the total number of species recorded in the district occurs here.

*Urban areas.* The urban areas lie to the east of the district, where they are concentrated in a narrow belt, approximately aligned to the coastline of the bay. Although less than 10% of the land falls into this category, it embraces a wide range of habitats.

The older parts of St. Ives, clustered around the harbour, lack gardens and as a consequence have little attraction for molluscs. Away from the harbour a network of domestic gardens, cultivated patches and waste-ground begins to appear. The varied habitats associated with these sites support a diverse molluscan fauna. Much the same pattern is continued at Carbis Bay and in the northern corner of Lelant included in this survey, although here the gardens tend to be larger and the green spaces more evident. Throughout the whole urban area, roadside verges, and to a lesser extent playing fields and cemeteries, provide important habitats for some species of snails.

The soil is normally less acid than that found on the farmland and elsewhere. This is most evident in the cultivated gardens where colour indicator readings of pH 7 and over are common.

*Freshwater habitats.* The narrow peninsula precludes streams of any importance from occurring and as the higher ground lies much closer to its northern coast, most streams in the district are less than 2 km in length. They are never very wide and because of the rapid descent from the moorland, relatively swift flowing; their beds strewn with water worn boulders and rocks. On the more level stretches gravel occurs, usually in the form of decomposed granite, and only a few slow-flowing ditches on the farmland have muddy bottoms.

Marshland is common throughout the district. Small stagnant bogs, completely devoid of molluscs, are occasionally found on the moorland. Slightly less acid marshes lie at the base of the hills, in which a few species of snails are found. There are also numerous waterlogged pastures which occur frequently on the farmland. Many of these dry out in the summer months; nevertheless, they constitute an important habitat for freshwater molluscs.

The largest expanse of still water is the small reservoir at Bussow. It is devoid of weeds and has a poor molluscan fauna; two species of *Pisidium* (*nitidum* Jenyns and *subtruncatum* Malm) and *Potamopyrgus jenkinsi* (E. A. Smith). Ponds are scarce, with only one of any importance for molluscs; an overflow pond connected to Bussow Reservoir, which regulates the amount of water available. The pond frequently dries out in the summer. Despite this it contains four species of *Pisidium*, in addition to *P. jenkinsi* and *Lymnaea peregra* (Müller).

## DISCUSSION

The granite acid back-bone of the peninsula, covered with extensive tracts of moor and farmland, does not provide a very congenial environment for molluscs. Surrounded by the sea on three sides, it is an exposed and windswept place, where the only shelter lies in the narrow steep-sided valleys. The area has an impoverished natural ground cover, which accentuates the importance of the Cornish 'hedges' as a habitat for many forms of animal and plant life, including snails. Some of these disadvantages are to a certain extent ameliorated for Mollusca by the frequent high humidity in summer and the mild wet winters. Nevertheless, the extreme SW of England does not possess an extensive molluscan fauna and is particularly deficient in freshwater species.

The preponderance of acid and exposed habitats manifests itself most clearly in the small size and poor condition of many shells. Small shells are common, several species reach no more



than the minimum adult dimensions, for example, *Clausilia bidentata* (Strom), *Balea perversa* (L.), *Candidula intersecta* (Poiret), *Ceriuella virgata* (Da Costa), *Lymnaea truncatula* (Müller) and *Lymnaea peregra* (Müller). *Helix aspersa* and *Cepaea nemoralis* (L), in particular, frequently have most of the periostracum eroded away by the action of the wind; while *Lymnaea glabra* (Müller) and *Lymnaea peregra* are often decollate, due to the acid habitats in which they live.

The area covered by this survey is contained within the ten-km grid squares SW 43 and 53 in the *Atlas of the non-marine Mollusca of the British Isles* (Kerney, 1976). Squares SW 44 and 54 are included in the survey area, but are mostly expanses of sea and are not treated separately in the *Atlas*. Sixteen additional species of molluscs, which have not been found in the present survey, are recorded by Kerney from SW 43 and 53. A high proportion of these appears to have been recorded solely from the dunes on the eastern side of St Ives Bay, from Hayle to Gwithian (SW 53 and 54, but both shown as SW 53 in the *Atlas*). These species are – *Carychium minimum* Müller agg. (pre 1950); \**Ovatella myosotis* (Draparnaud); \**Pupilla muscorum* (L.); \**Vallonia pulchella* (Müller) (19th C. record considered by Stella M. Turk to be erroneous and referring to *V. excentrica* Sterki); *Vallonia excentrica* Sterki; \**Ena obscura* (Müller); *Aegopinella pura* (Alder); *Zonitoides nitidus* (Müller); *Cecilioides acicula* (Müller); \**Zenobiella subrufescens* (Müller); \**Arianta arbustorum* (L.) (recorded live near Morvah, 12 km west of St Ives); *Lymnaea palustris* (Müller); *Lymnaea stagnalis* (L); *Anisus leucostoma* (Millet); *Gyraulus albus* (Müller); and *Sphaerium lacustre* (Müller). Those species marked with an asterisk refer to 19th century records, mostly collected from 'beneath the surface of the Towans', and may be of sub-fossil origin. *L. stagnalis*, *A. leucostoma* and *S. lacustre* have only recently been found live in SW 53 and are not shown in the *Atlas*.

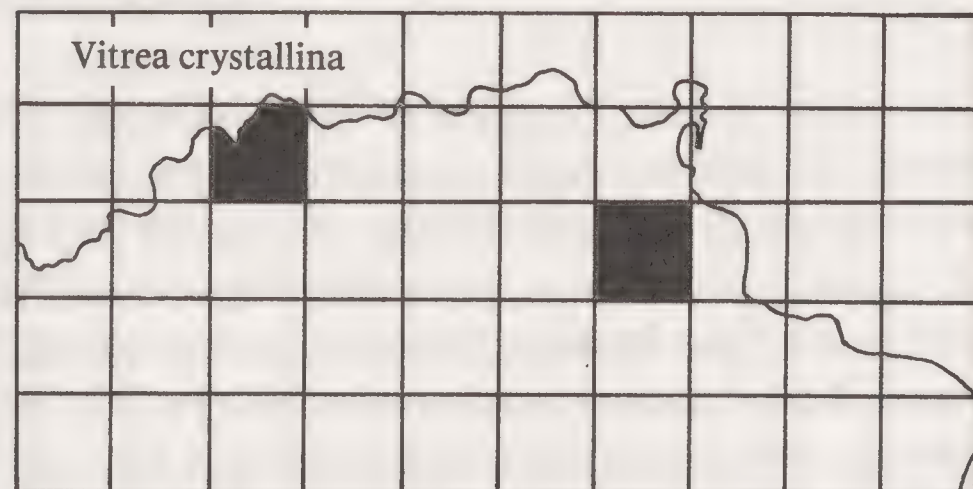
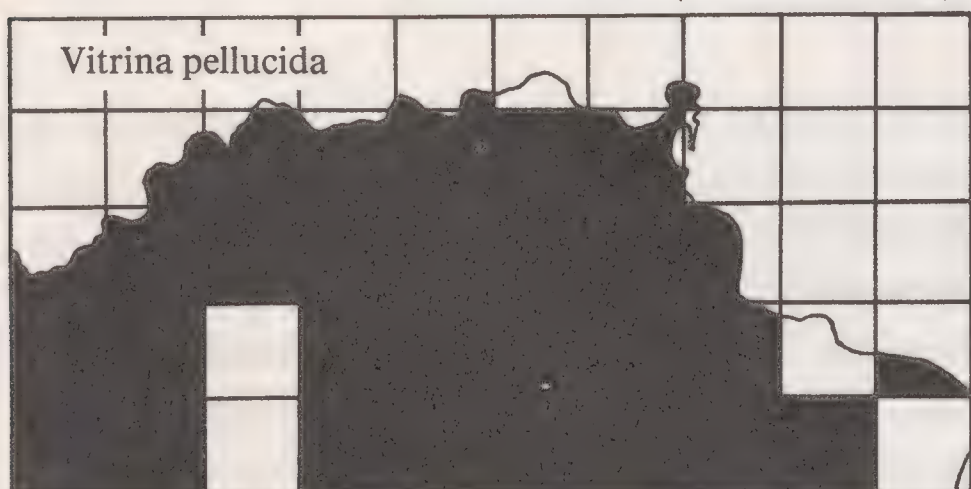
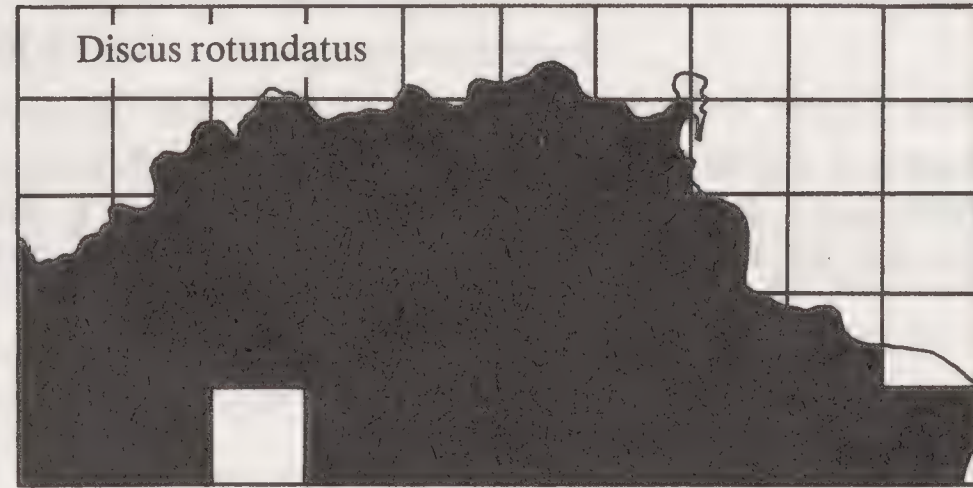
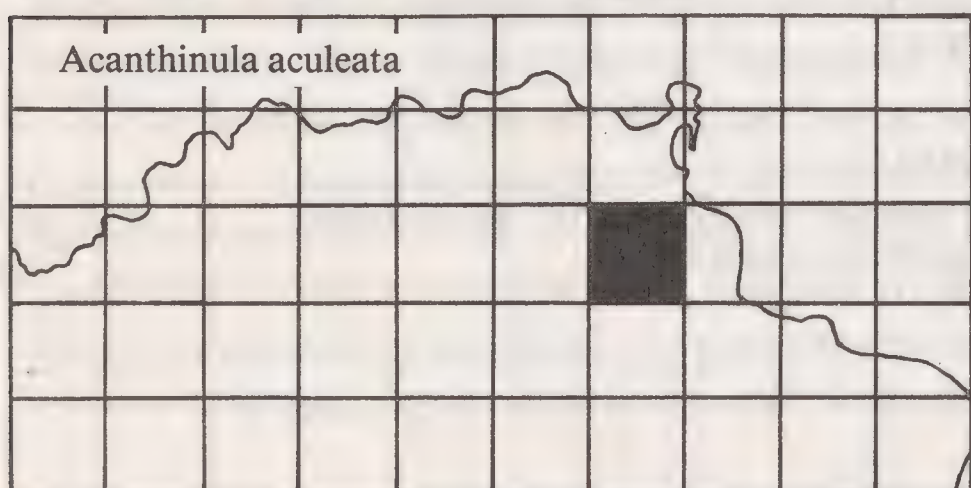
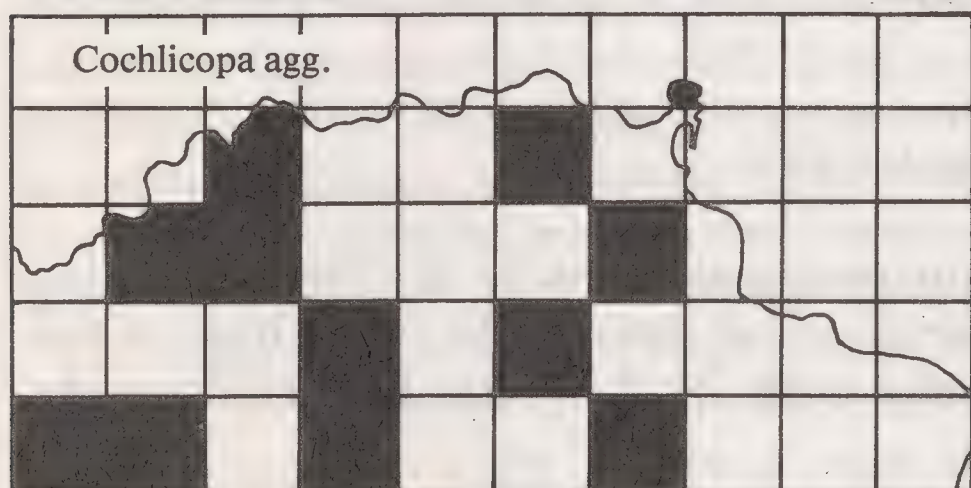
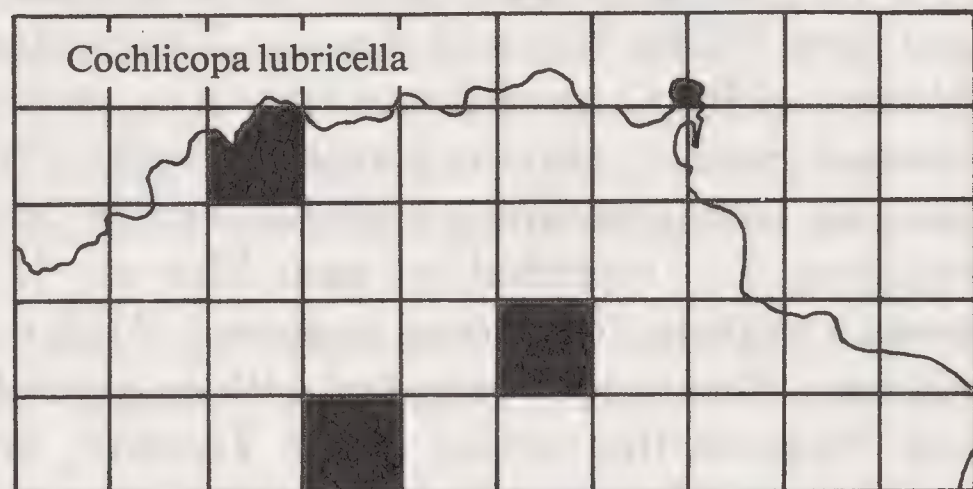
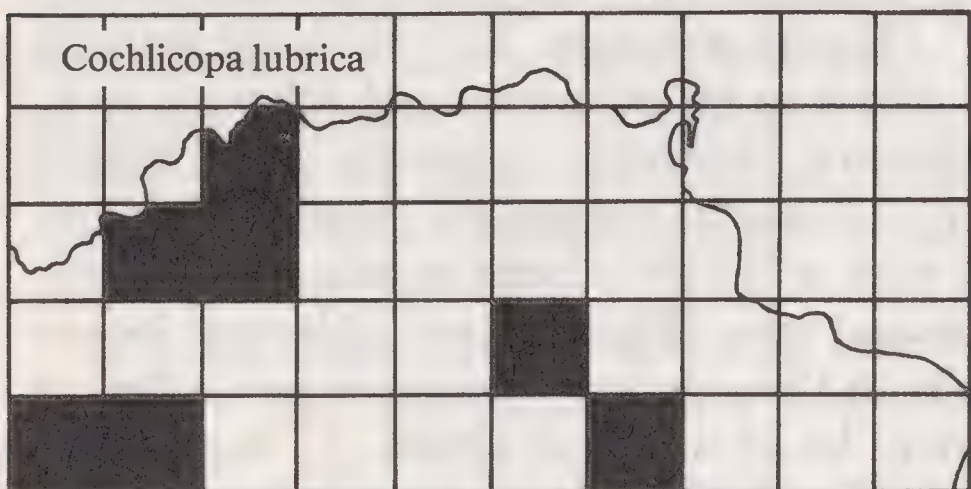
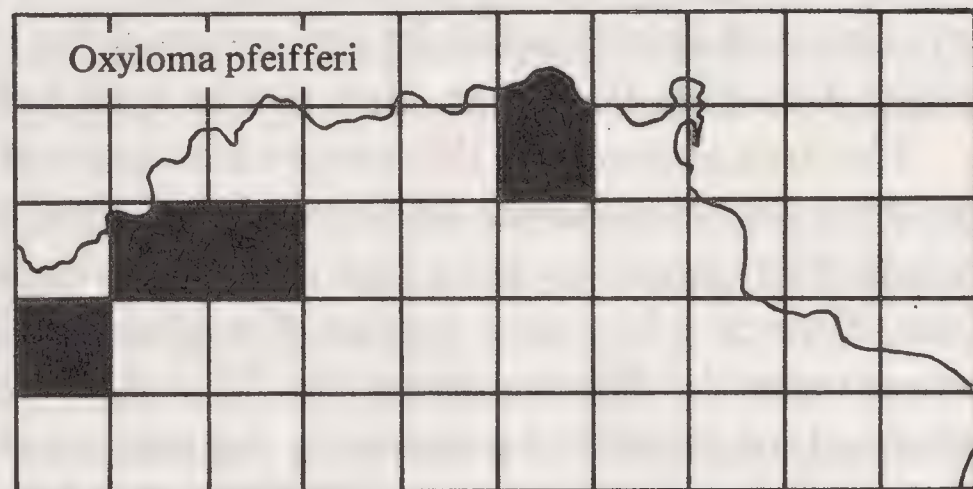
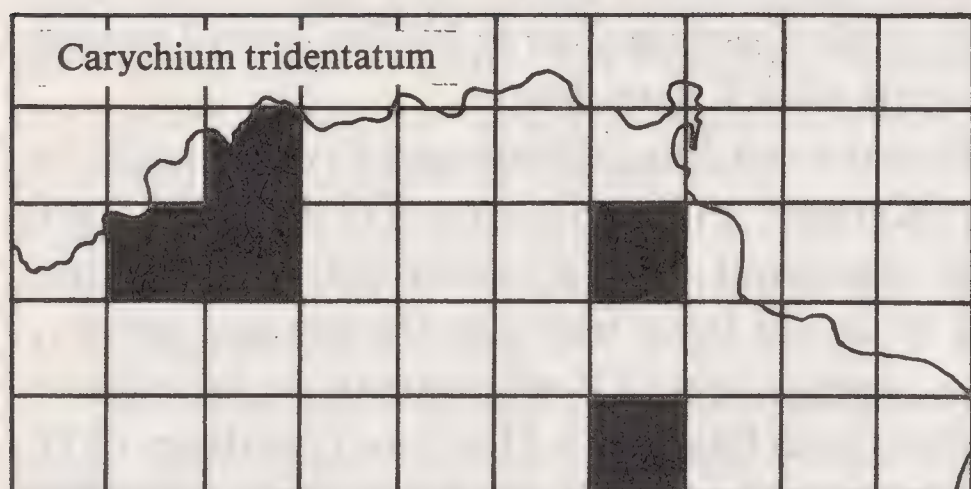
#### ACKNOWLEDGEMENTS

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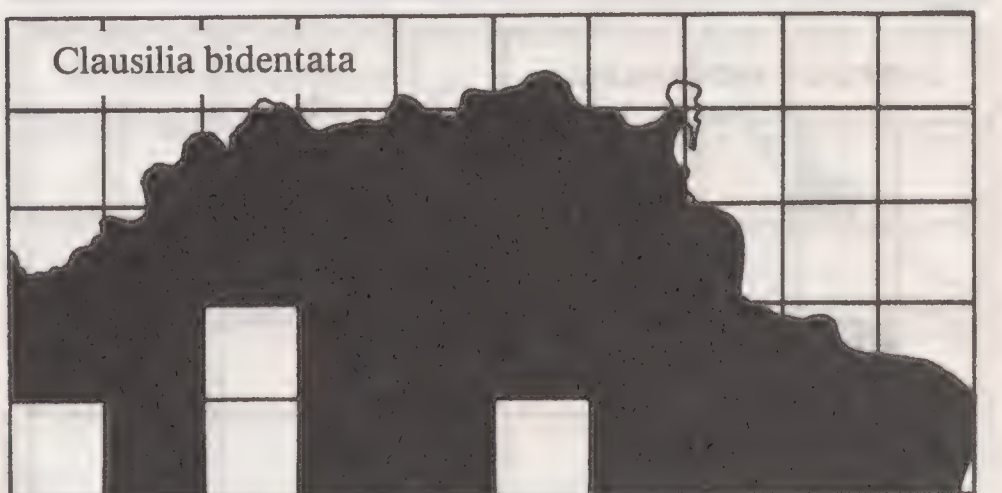
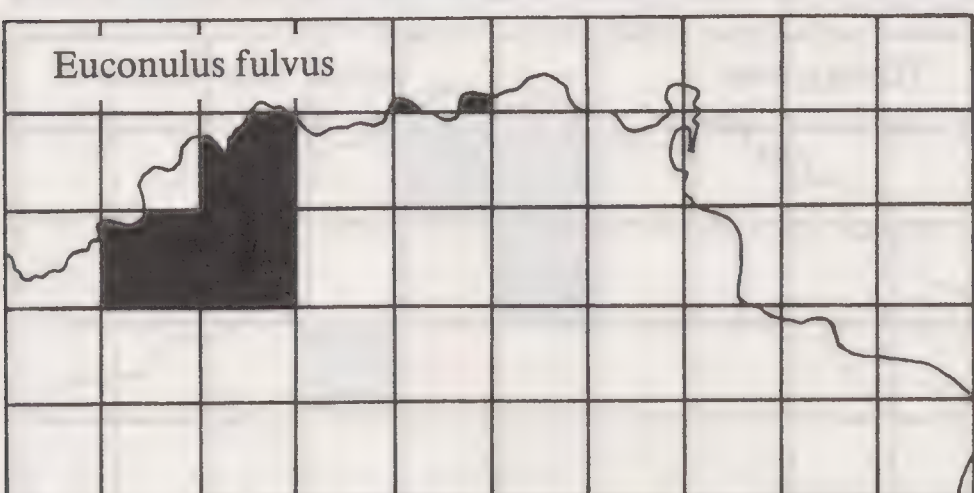
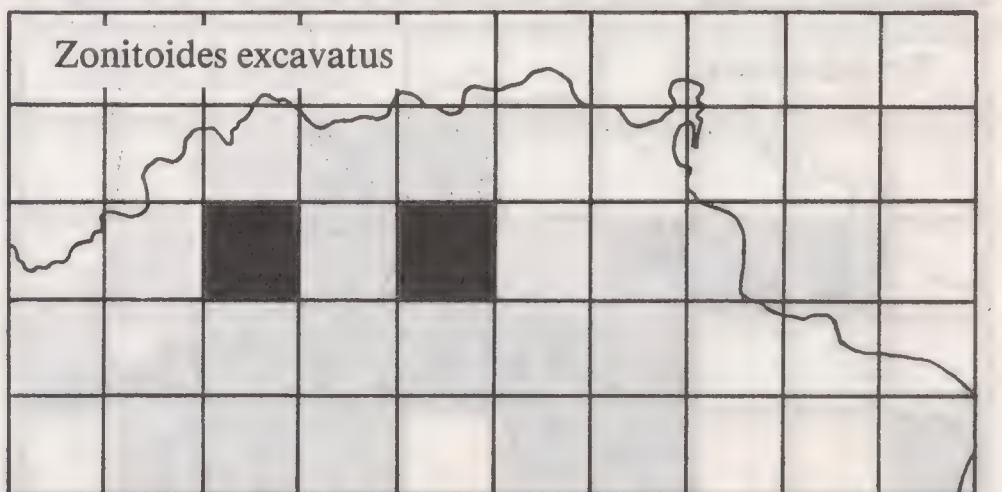
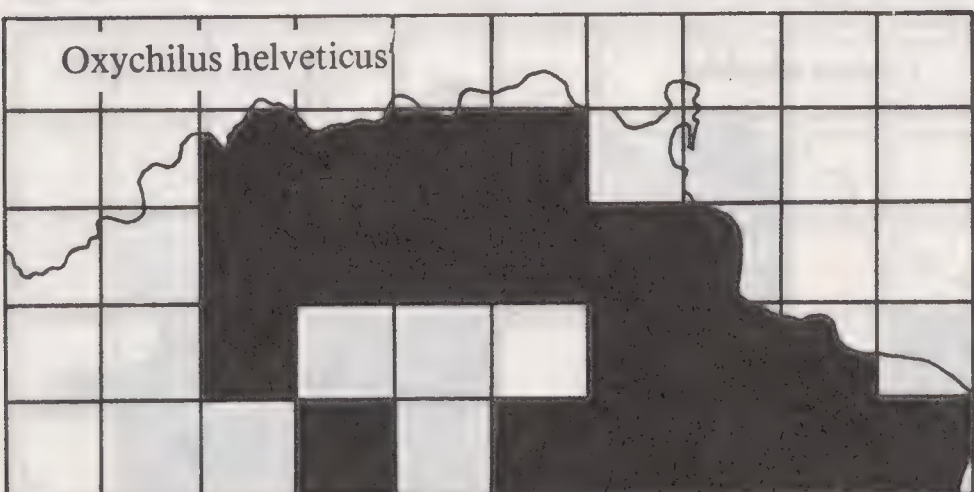
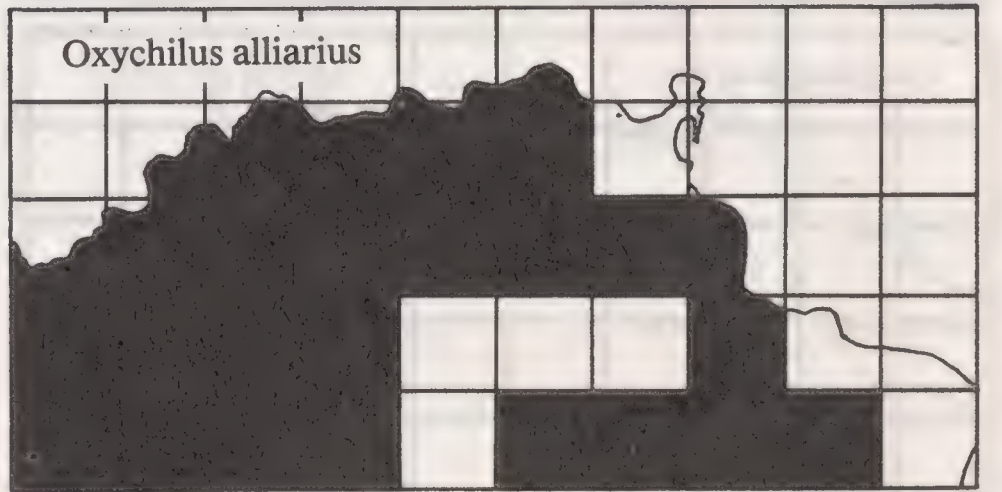
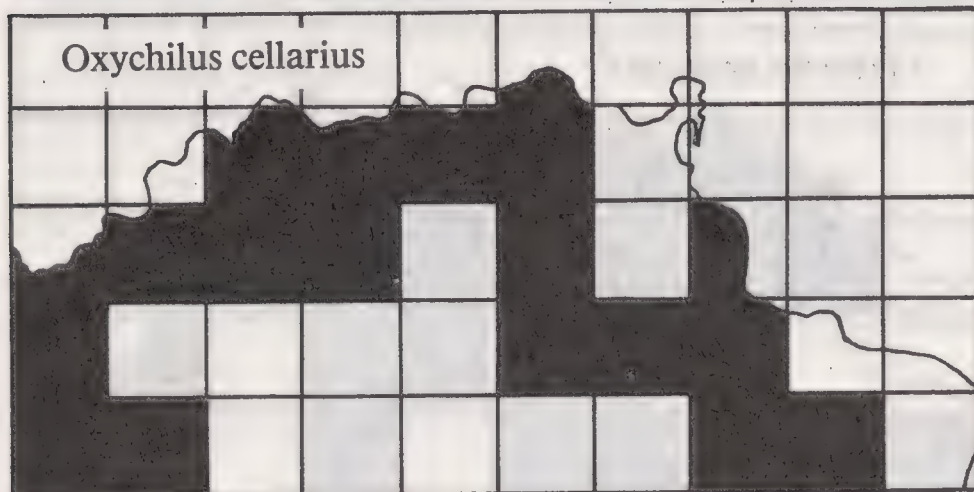
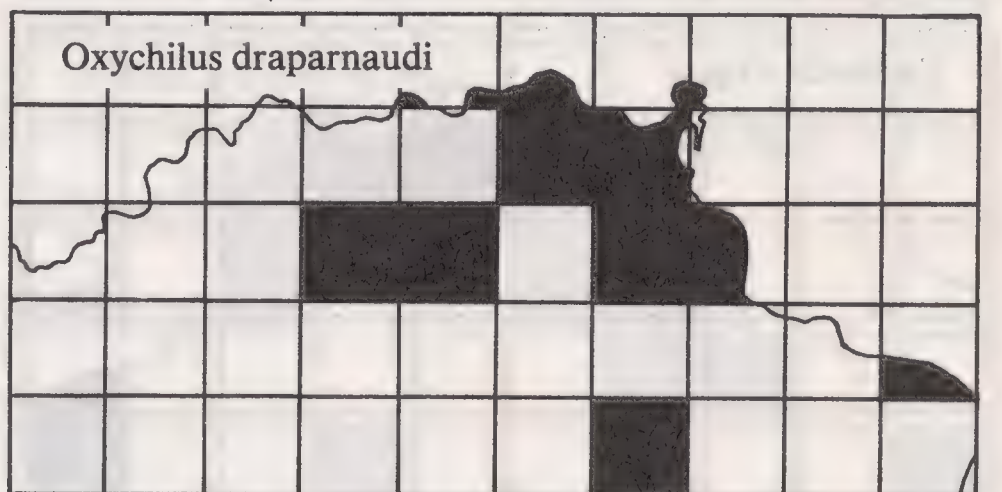
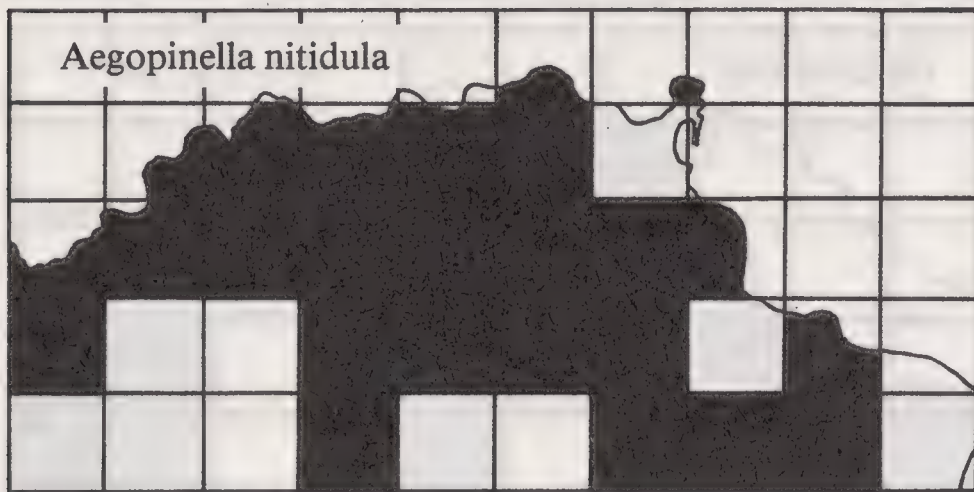
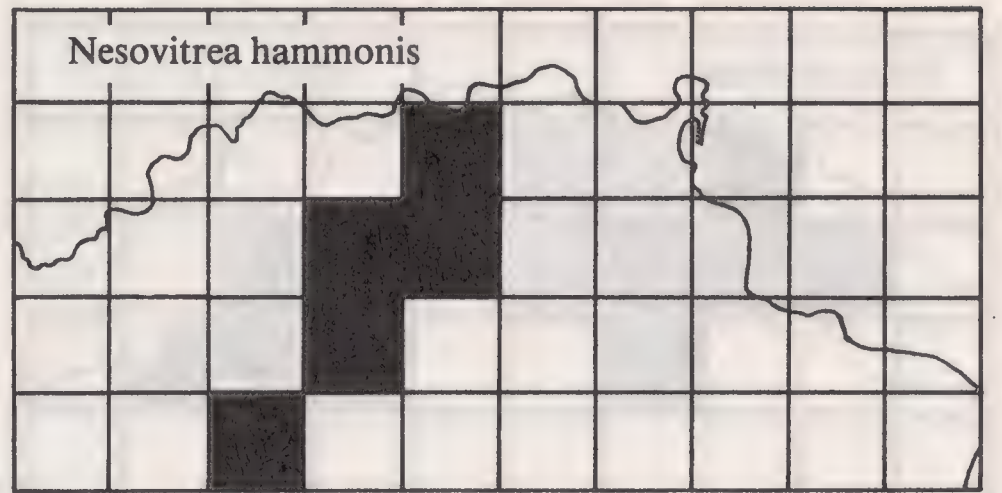
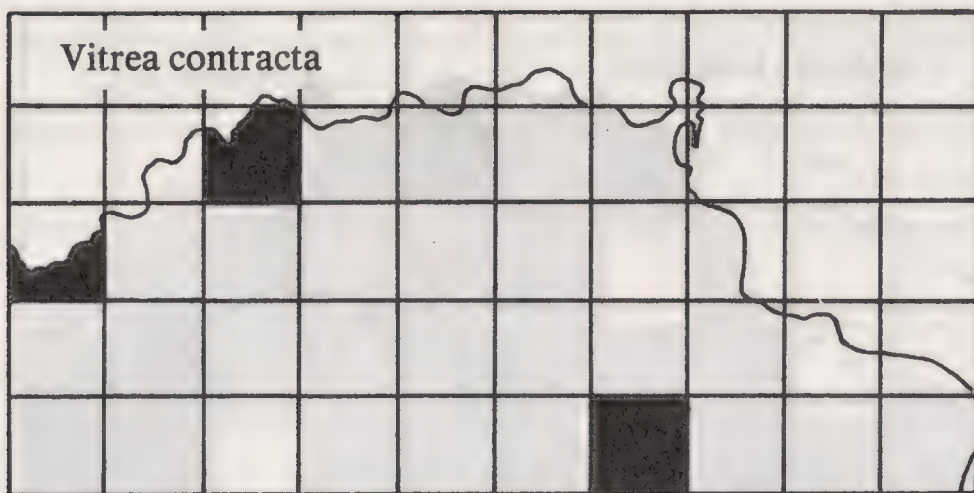
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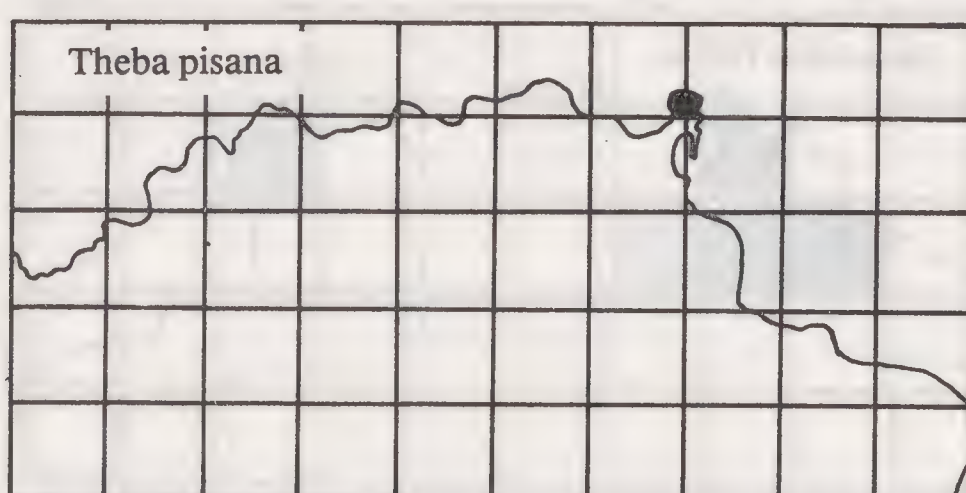
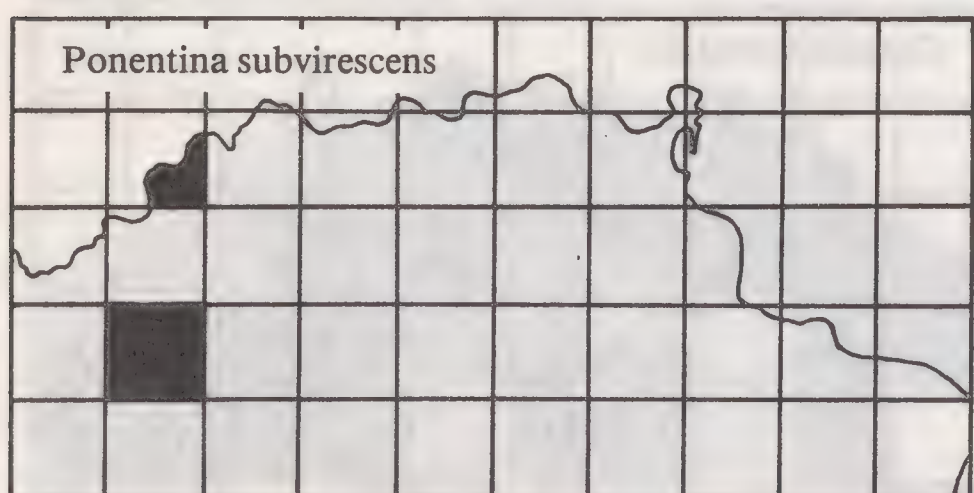
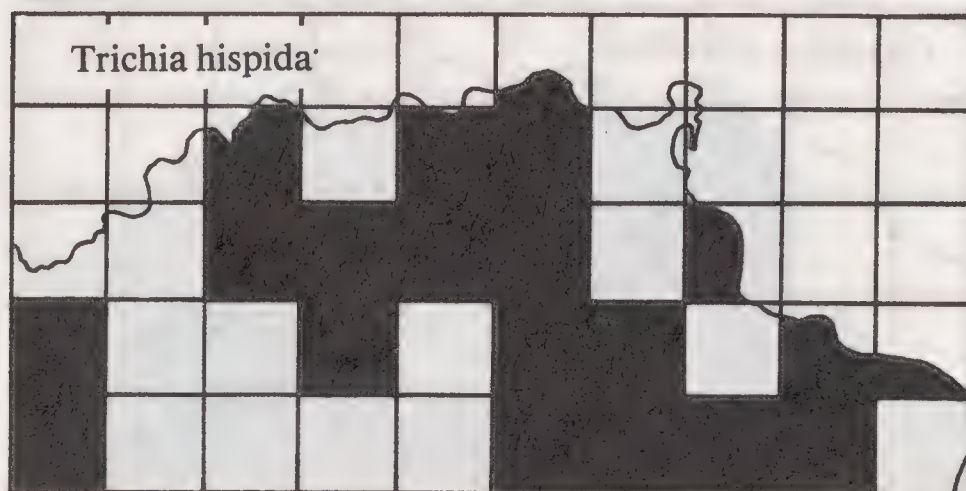
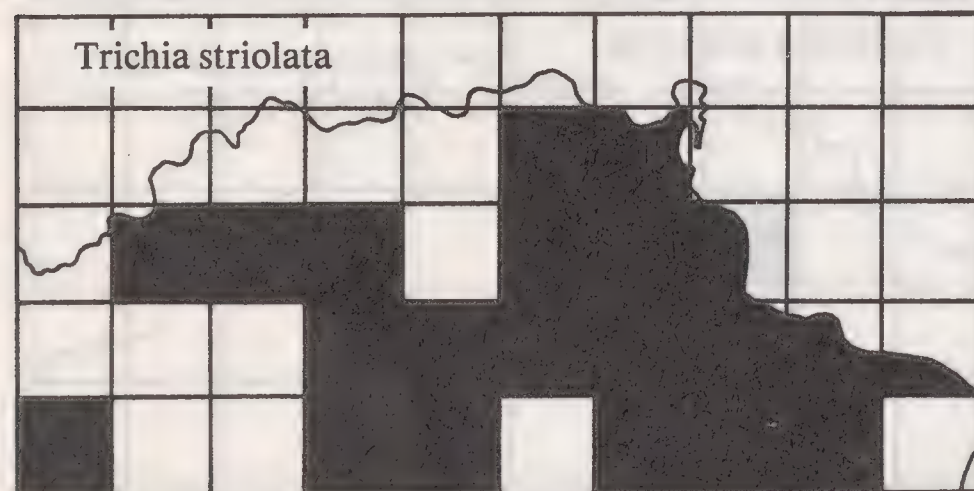
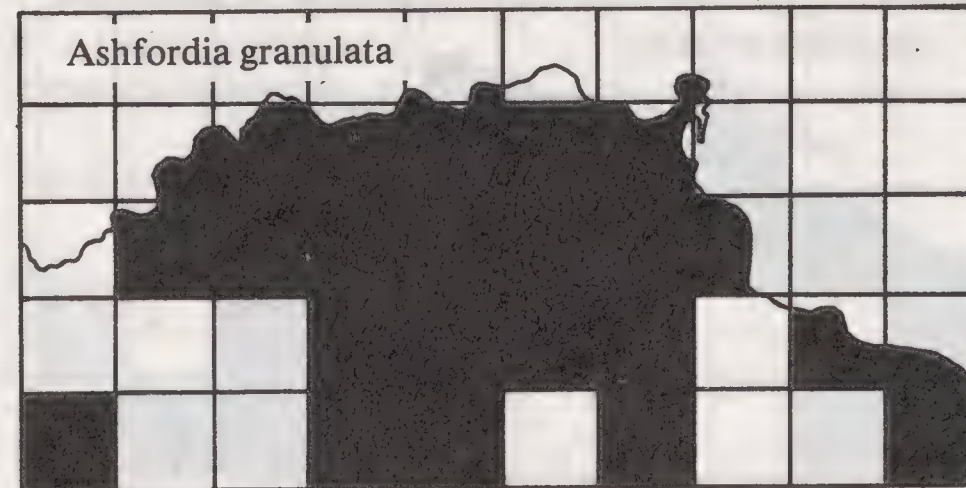
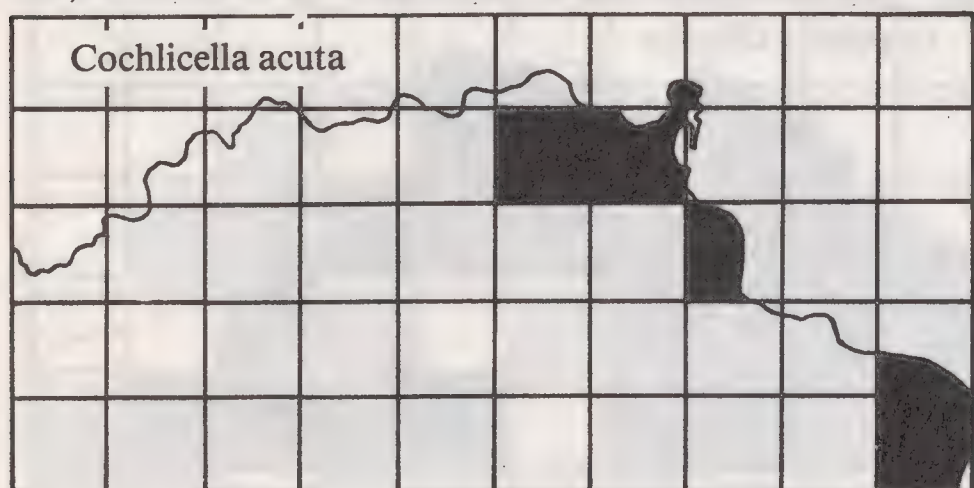
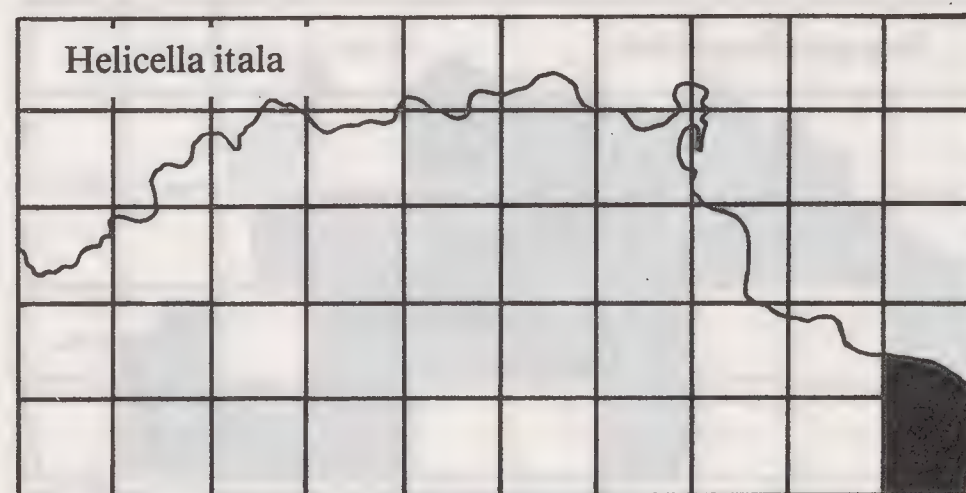
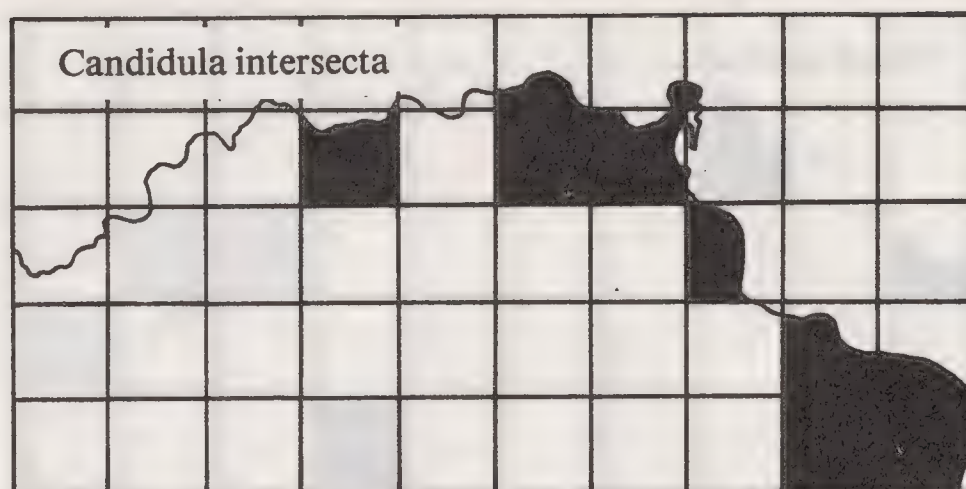
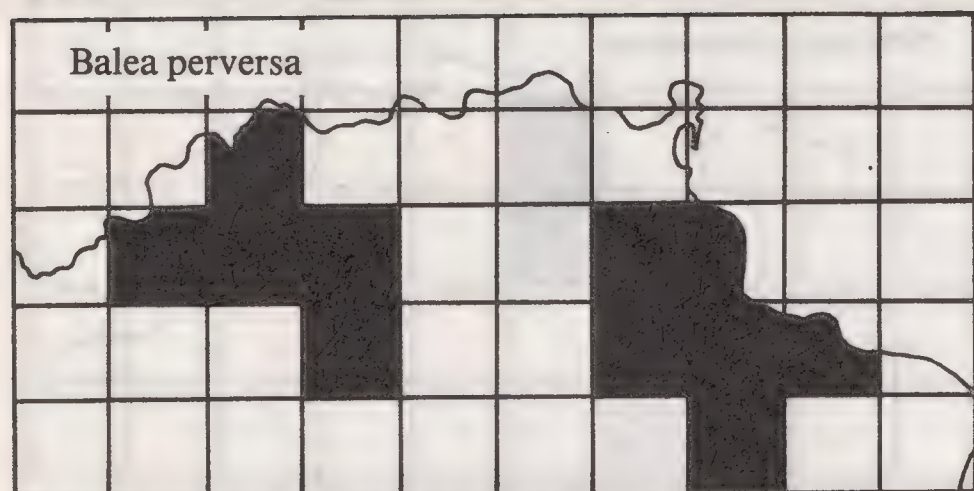




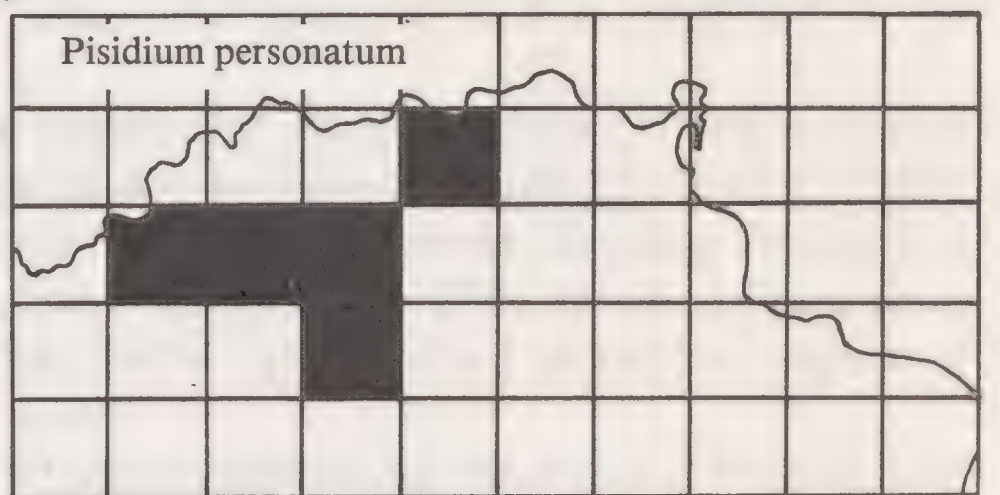
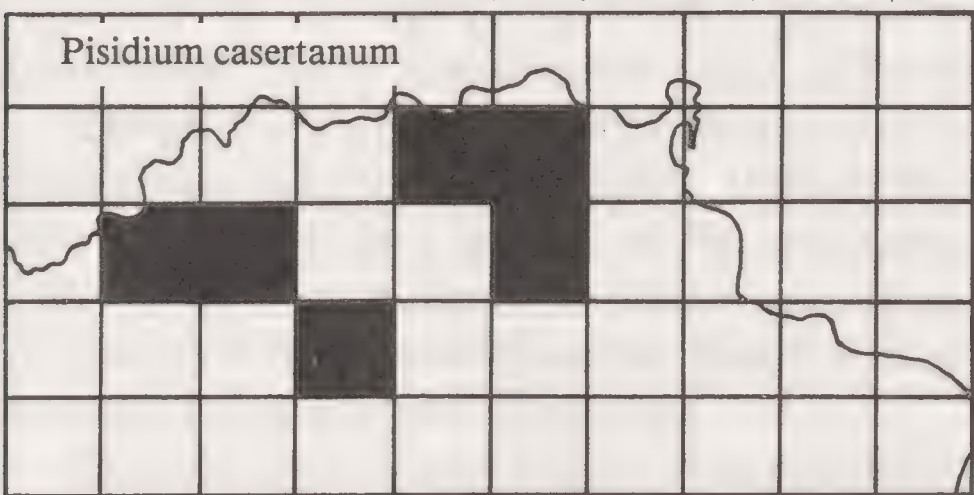
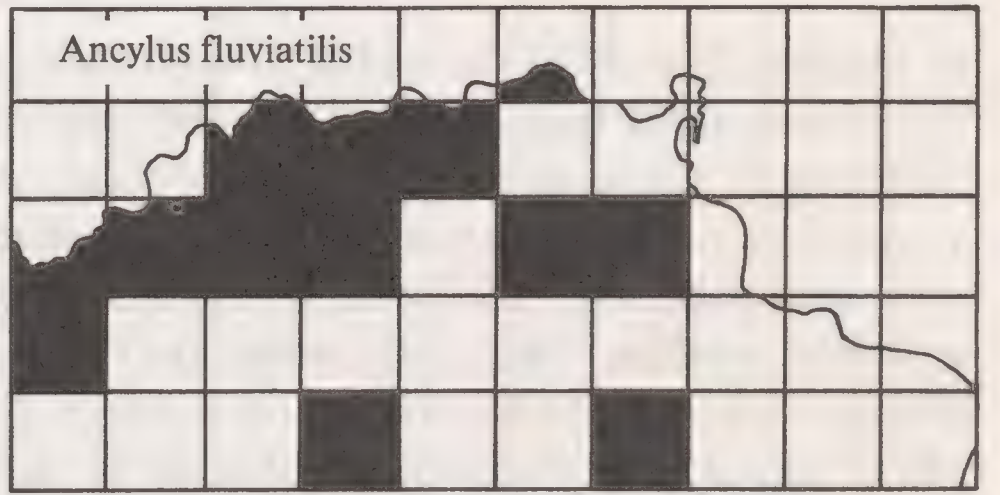
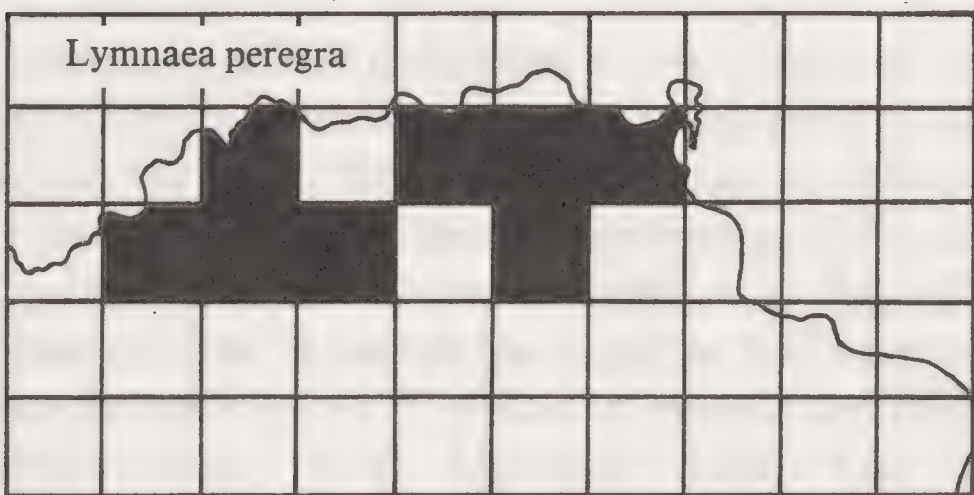
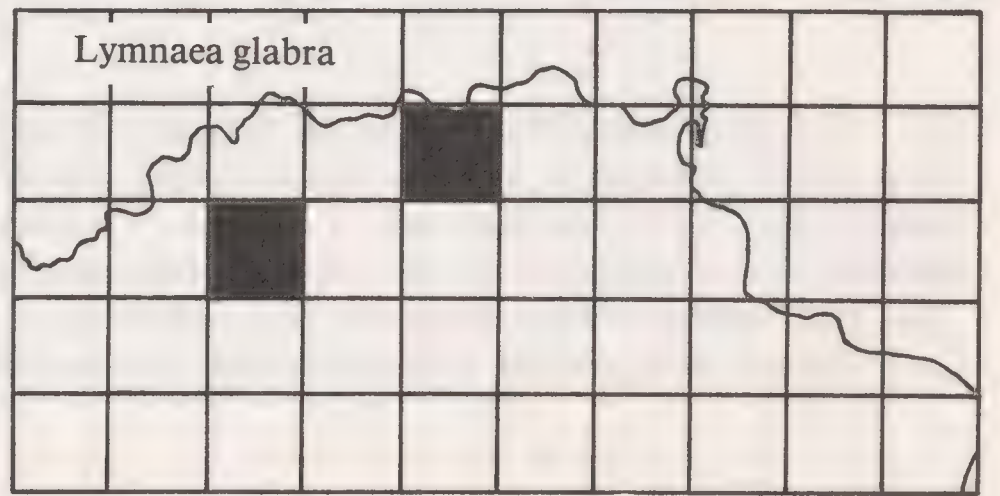
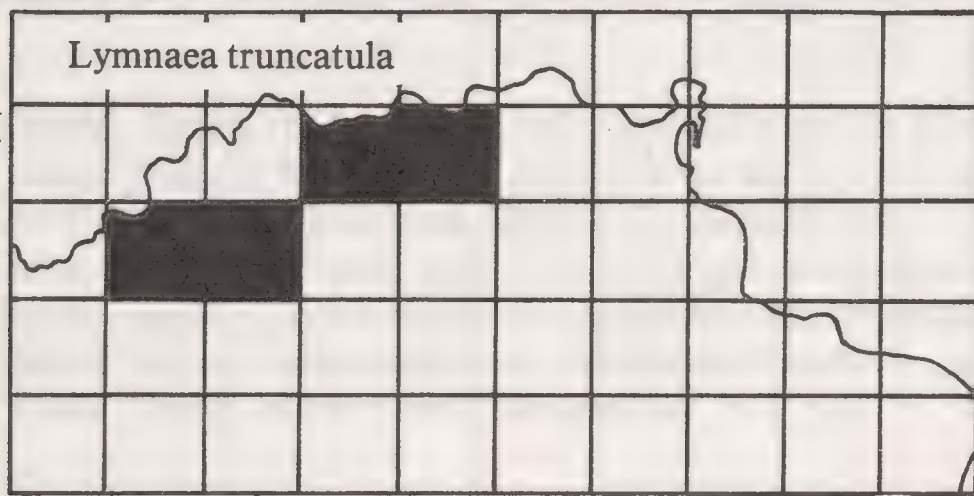
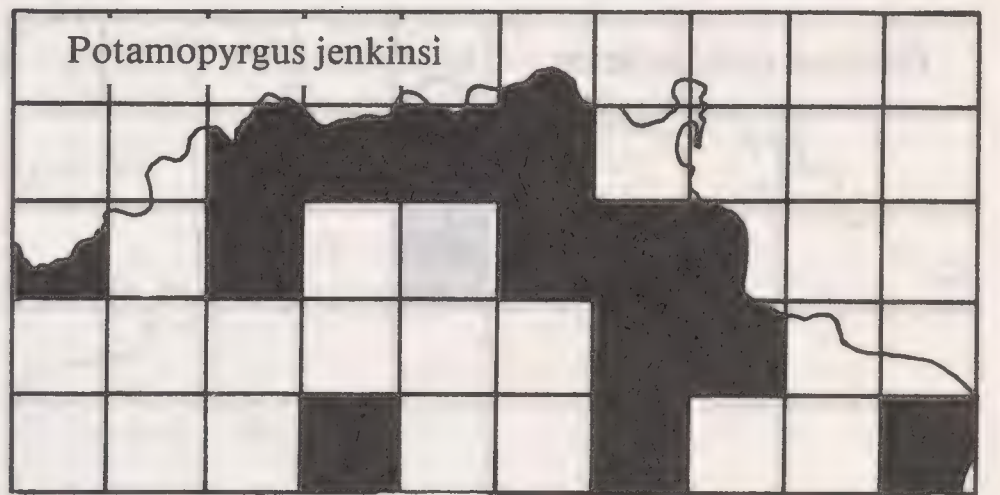
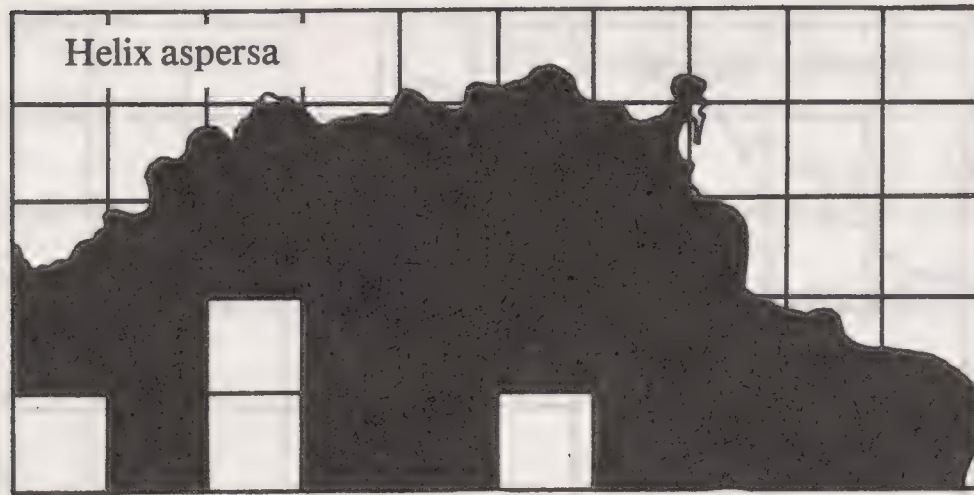
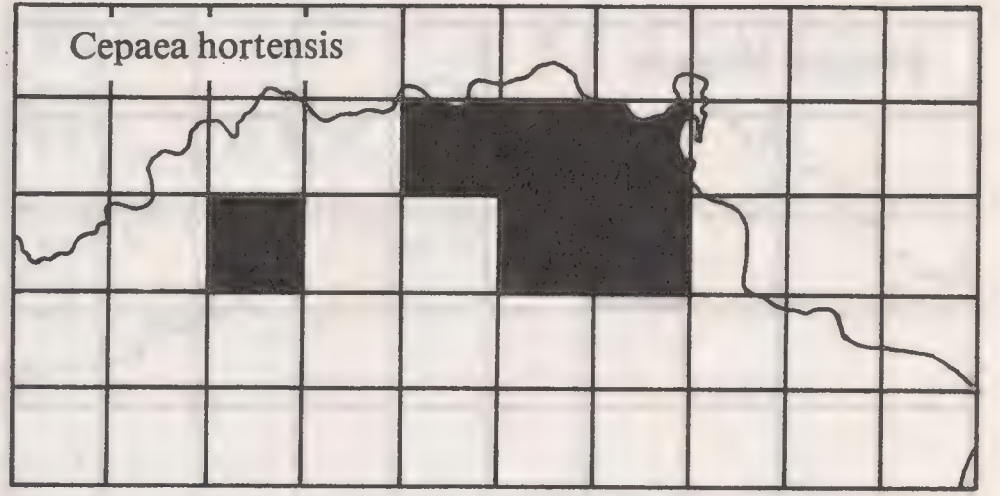
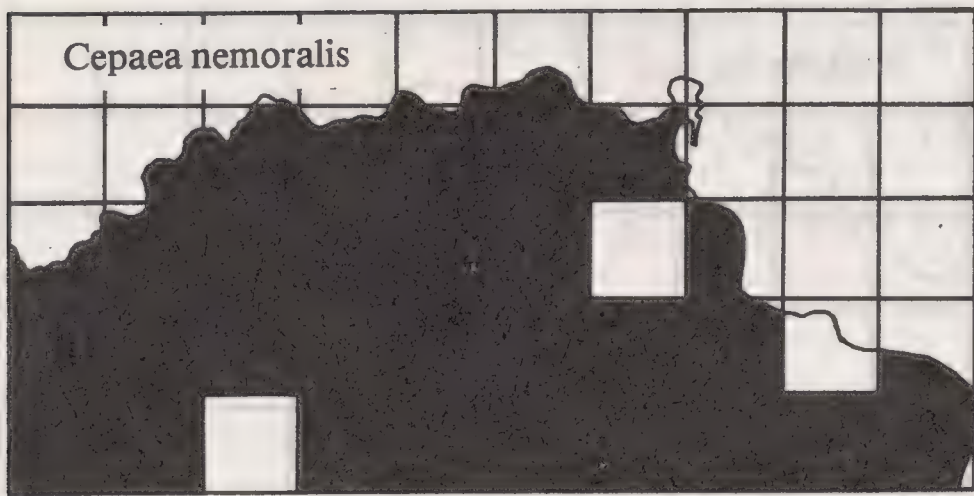




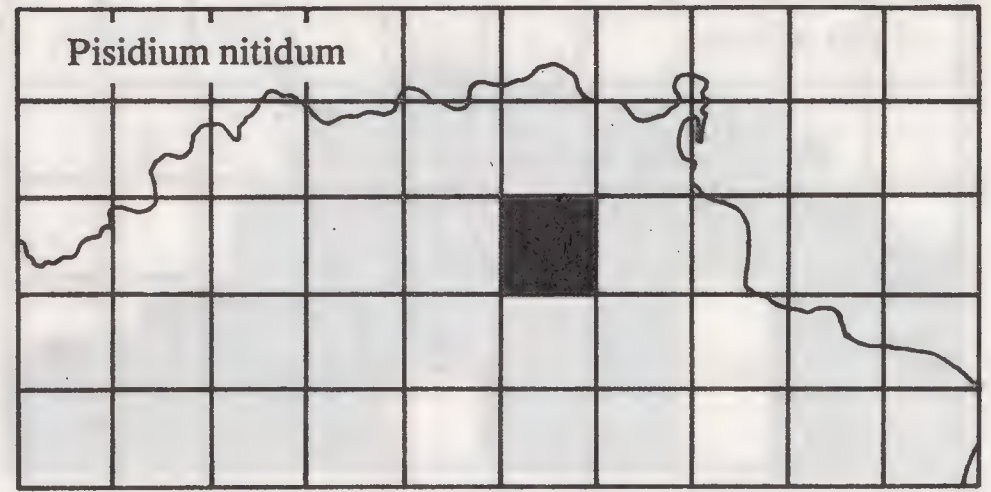
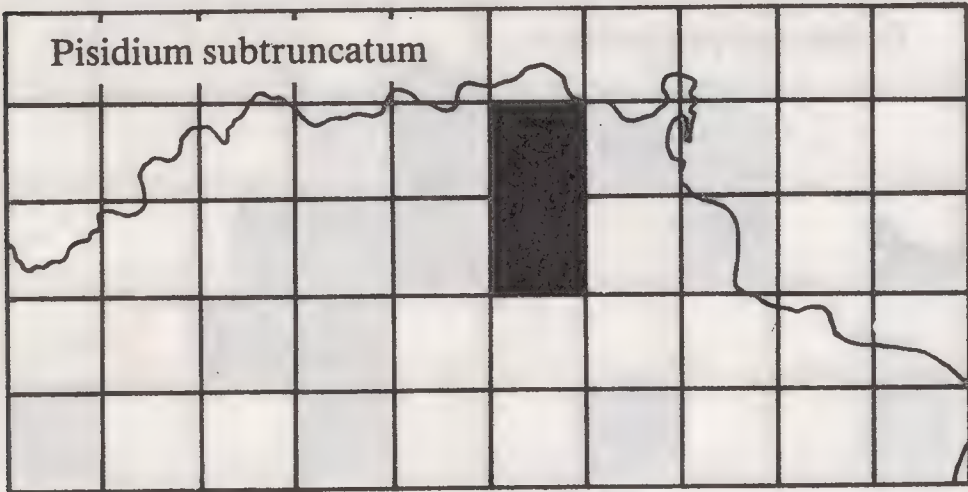
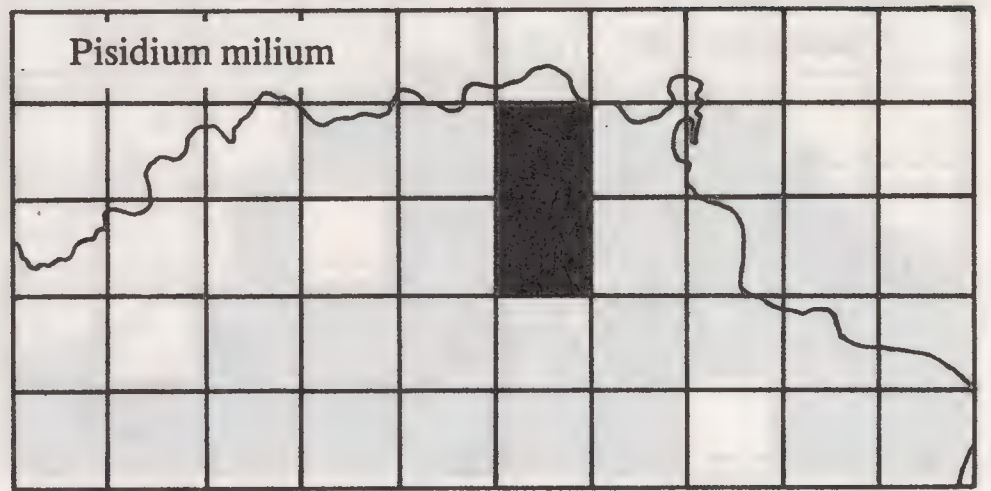
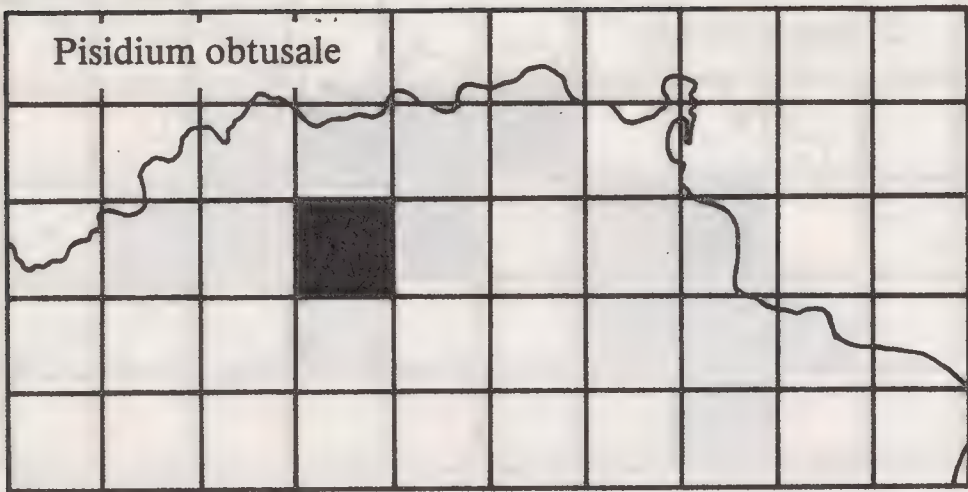














# A REDESCRIPTION OF *PLACIDA VIRIDIS* TRINCHESE, 1873 (GASTROPODA: ASCOGLOSSA)

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*Abstract:* *Placida viridis* is a little known Mediterranean ascoglossan that has not been examined in detail since 1893. The redescription includes new observations on the reproductive system, central nervous system, and radula; it points out that the animal lacks a heart. We hope it will help collectors who find *P. viridis*, or a related species, on the coasts of other continents to come more surely to a decision. The evidence presented indicates that *Placida* (type species, *Placida viridis* Trinchese, 1873) can no longer be regarded as a subgenus of the genus *Hermaea* [type species, *Hermaea bifida* (Montagu, 1844)]. It is recommended that the genus *Hermaea* be transferred to a restricted family Hermaeidae and the genus *Placida* remain in the family Stiligeridae.

Trinchese (1873) published a description of *Laura viridis* n.spec., n.gen. In 1879 he illustrated its external features by a splendid coloured plate. By this time he had changed the name of the genus to *Placida*, because Lacaze-Duthiers had used *Laura* for a parasitic crustacean, *L. gerardiae*. Trinchese collected his first specimens of *Placida viridis* near a jetty at the port of Genoa. Twenty years later he found several more in the Bay of Naples and this enabled him to publish some new observations. A search through the literature revealed that, since 1893, little has been added to our knowledge of *P. viridis*. A reason for this may be that it is a rare Mediterranean species (Pruvot-Fol, 1954). However, Sordi and Majidi (1956) reported that it is found fairly frequently at Livorno; and Sordi suggests that it may well occur at several localities, as yet unrecorded, along the western coast of Italy.

There are many references to the systematic position of *Placida*. Bergh (1878) regarded *Placida* as a subgenus of *Hermaea*, though he appears not to have examined *P. viridis*. Thiele (1931) placed it in a section of *Physopneumon*, which is but a synonym of *Hermaea*. Pruvot-Fol (1954) sought to re-establish *Placida* as a separate genus. Thompson (1976) classified *Placida* as a subgenus of *Hermaea* within the family Stiligeridae. Baba (unpublished world-list) regarded *Placida* as a genus of Stiligeridae.

The redescription of *Placida viridis* enabled us to form an opinion on the status of *Placida*. The new evidence presented suggests that the genera *Placida* and *Hermaea* are not closely related. To express this in taxonomic terms, it is recommended that *Placida* remain in the family Stiligeridae and *Hermaea* be placed in a restricted family Hermaeidae. Arguments in support of this change are given in the discussion.



## EXTERNAL FEATURES

*Placida viridis* (Fig. 1) is an eolidiform ascoglossan of length 15–20 mm and breadth 1–2 mm. The ground colour of its skin is a semitransparent greyish white. As in *Placida dendritica* (Alder and Hancock), green branches of the gut are visible through the dorsal surface, including the rectal spout and tentacles; some branches extend along the sides of the body. The green colour is due to chloroplasts from the cell-sap on which it feeds. As digestion proceeds the colour fades; and if an animal be starved for two or three days, the branches of the gut become almost colourless. Long-term chloroplast symbiosis is therefore unlikely.

Flecks of a dark reddish-violet pigment are distributed over the dorsal surface; they line the edges of the tentacles, the border of the foot, and darken the sides of the head. Some are scattered over the cerata, each of which is usually tipped with dark violet. Two fine-grained stripes of the same colour run along the sole of the foot (Fig. 1B,vs); these easily distinguish *Placida viridis* from *P. dendritica* which it otherwise closely resembles in external features.

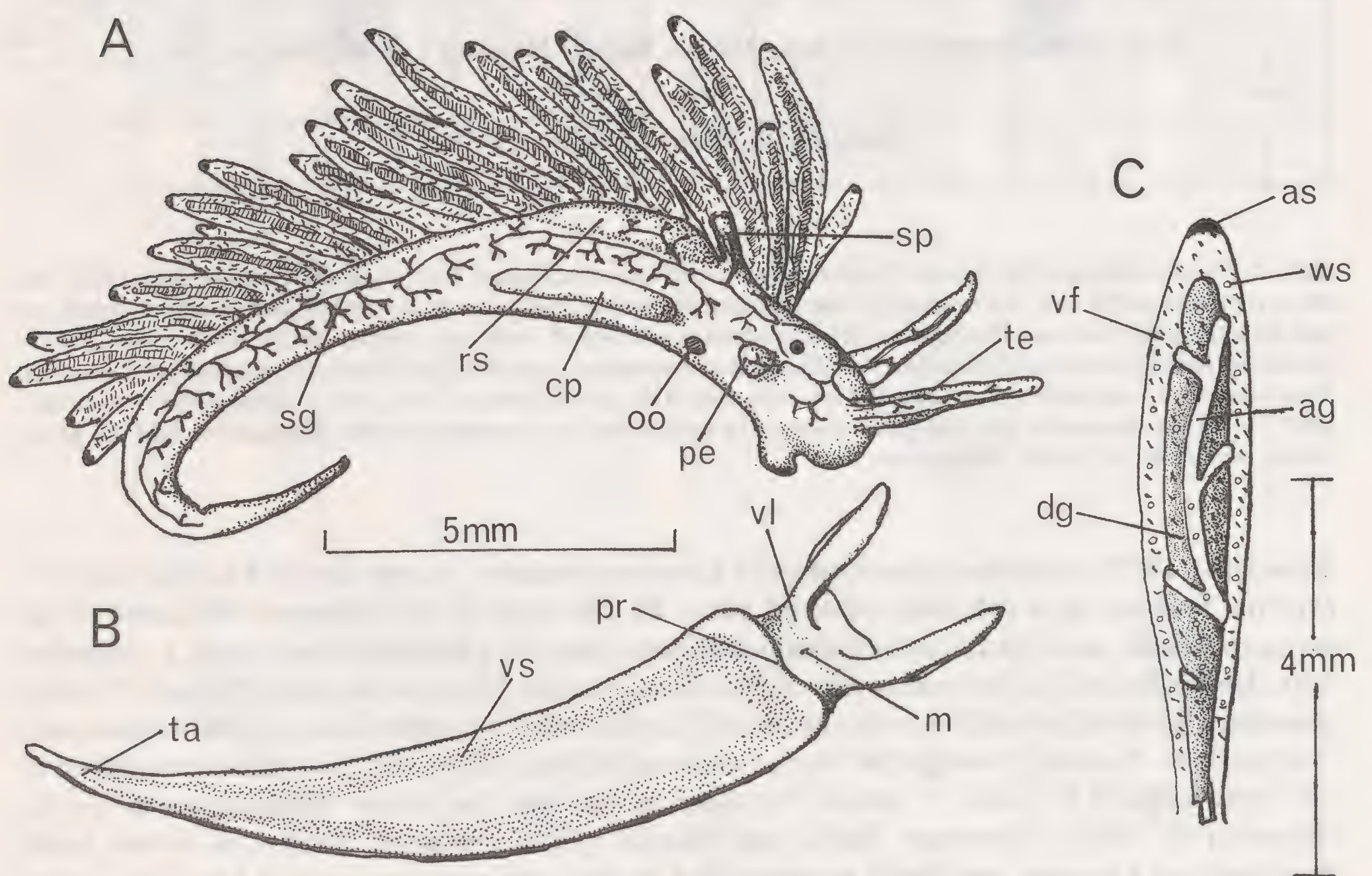


Fig. 1. External features of *Placida viridis*. A preserved specimen, cerata of right side removed. B ventral view of foot. C a cerata. ag albumen gland; as apical spot; cp copulatory pad; dg diverticulum of gut; m mouth; oo oviducal opening; pe penis; pr pedal notch; rs renal swelling; sg subcutaneous gastric branch; sp anal spout; ta tail; te tentacle; vf dark violet fleck; vl velum; vs dark violet stripe; ws whitish spot.

About 40 fusiform cerata are arranged in rows along each side. They vary in size; some of the more median ones are about half the length of the body, and the most lateral are the smallest. Each cerata (Fig. 1C) contains an unbranched gastric diverticulum (dg) entwined by a branch of the albumen gland (ag). The cerata of *Placida dendritica* differ in that each diverticulum has short lateral branches. Fig. 2A is an anatomical drawing and gives a poor impression of the cerata. In living *P. viridis* they are more pointed and the larger ones maintain a more upright position than in most ascoglossans. When the animal is active the cerata are in continuous rhythmic motion;



in this it may resemble *Placida kingstoni*, a new species described by Thompson (1977). The cerata are highly contractile. Once a small crustacean scuttled along the back of a *P. viridis*. Immediately its cerata contracted close to its body; later they extended to their former length and recommenced moving rhythmically.

The tentacles are about 5 mm long, they are capped with white and tipped with violet; each has a fold facing outwards. Their median margins are continued on to the front of the head, above a bilobed velum (Fig. 1B, vl). The renal swelling is large and of a whitish, crystalline appearance. Adjacent and anterior to the renal swelling is the median anal spout (sp).

The penial opening (po) is on the right side about level with the eyes. A penis was not seen in living animals, though in 19 of 20 preserved specimens it was extruded with the cuticular style visible. The copulatory pad (cp) is an elongate swelling that commences posterior to the penial opening and extends 4–6 mm along the right side. The oviducal opening is ventrally placed between the pad and penial opening. A vaginal or bursal opening is not present.

The foot has a notch (pr) on its anterior border in line with the mouth. The pedal notch varies considerably in size; when the foot glides forward the notch is scarcely perceptible. The tail is tapered and of moderate length.

*Placida viridis* is found among filaments of *Bryopsis*. It is very difficult to locate because it is cryptic in form and colour. Sordi notes that *Placida dendritica* and *P. viridis* may be found on the same tuft of *Bryopsis*. Since the two species have similar genitalia, hybrid individuals are a possibility. It may be that *Placida brevirostris* and *P. tardyi*, species named by Trinchese (1873), were hybrid forms.

**Field identification characters.** Length, 15 to 20 mm – of slender form – numerous fusiform cerata tipped with dark violet pigment – green branches of gut visible through the skin over the dorsal surface and tentacles – *two fine-grained stripes of dark violet along the sole of the foot.*

#### INTERNAL ANATOMY

*Alimentary System* (Fig. 2) *Placida viridis* feeds on green filaments of *Bryopsis*. When feeding it grasps a filament firmly in the pedal notch and lowers its head which contracts so that the filament is aligned across the mouth, and held in a groove between the lobes of the velum. The lower limb of the radula now acts as a lancet and its leading tooth pierces through the wall of the filament. The contents are then sucked out by the pumping action of the buccal mass. When the animal moves away it leaves behind an empty section which, if carefully examined, shows a slit (sm) and a grip mark (gm) as depicted in Fig. 2B.

Pedal gland cells open into a hollow, ventral to the mouth; and buccal gland cells surround a short oral tube. The long axis of the buccal mass is of length 700  $\mu\text{m}$ . The internal buccal muscles were illustrated by Trinchese (1893; Fig. 8); they are arranged as in *Caliphylla mediterranea*. *P. viridis* has five external ventral muscles which are not present in *P. dendritica* or *Hermaea bifida*. The radular elements of *P. viridis* form a single longitudinal row and are all retained on the radular ribbon which ends in a spiral inside the ascus. E1 and E2 are rudiments (Fig. 2D), E3 is a transitional tooth, and E4 is the first fully-formed tooth. It has a depression on the back extending from near the apex to the base of the tooth, and the margins of the cusp are smooth; this type of tooth is called awl-shaped. In an animal 15 mm long, the largest tooth was of length 127  $\mu\text{m}$  and the number of elements 24. Details of the salivary glands are shown in Fig. 2A. The wall of the oesophagus has an inner lining of ciliated cuboidal cells, a middle layer of gland cells, and an outer muscular coat. A thin-walled oesophageal pouch (op) is present; it has no middle layer of gland cells. The intestine (in) begins near the stomach; it ascends to the dorsal surface and is continued by the rectum along the anal spout (sp) to the anus (an).

The histology of the stomach (Fig. 2C) is similar to that of the oesophagus. Internally it has about 13 longitudinal folds with larger glandular cells and longer cilia. The median fold is larger than the rest, it is formed by an infolding of the wall, looks like a typhlosole (Fig. 2C, ty)



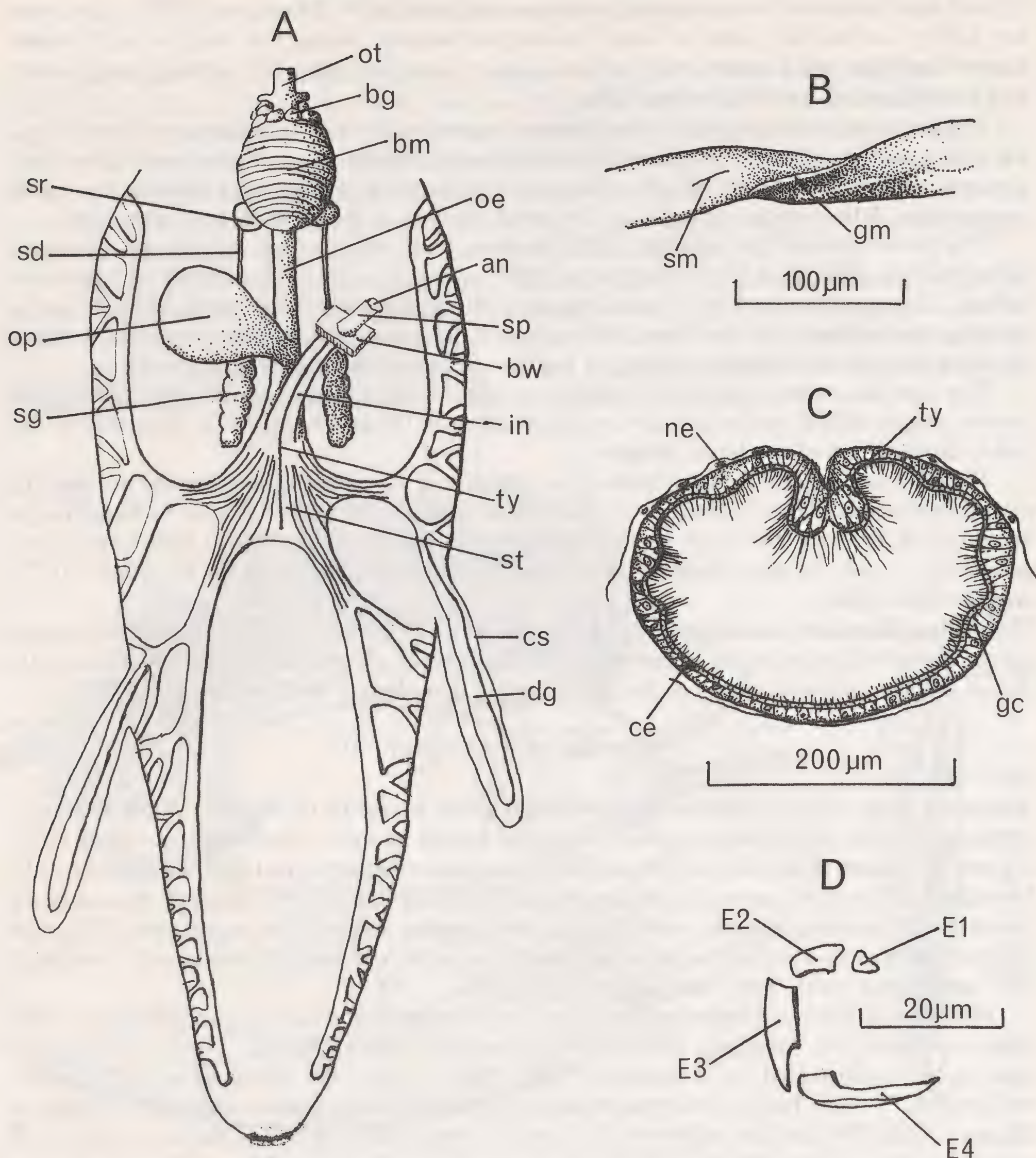


Fig. 2. A diagram of gut. B part of a *Bryopsis* filament on which *P. viridis* had fed. C transverse section of stomach near the beginning of intestine. D first four elements of radula. an anus; bg buccal gland; bm buccal mass; bw body wall; ce ciliated endothelium; cs ceras; dg gastric diverticulum; E1-E4 radular elements; gc gland cells; gm grip mark; in intestine; ne nerve; oe oesophagus; op oesophagael pouch; ot oral tube; sd salivary duct; sg salivary gland; sm slit mark; sp anal spout; sr salivary reservoir; st stomach; ty typhlosole.

and is continued along the intestine. Two lateral trunks arise from the sides of the stomach and subdivide into branches that each supply a few cerata, as in *P. dendritica* and *Alderia modesta*.

*Reproductive system* (Fig. 3). Ascoglossans are simultaneous hermaphrodites and fertilization is internal. During mating the partners exchange sperm which is then stored in a pouch (bursa copulatrix) while the eggs mature. Eggs and sperm develop, side by side, in an ovotestis of many



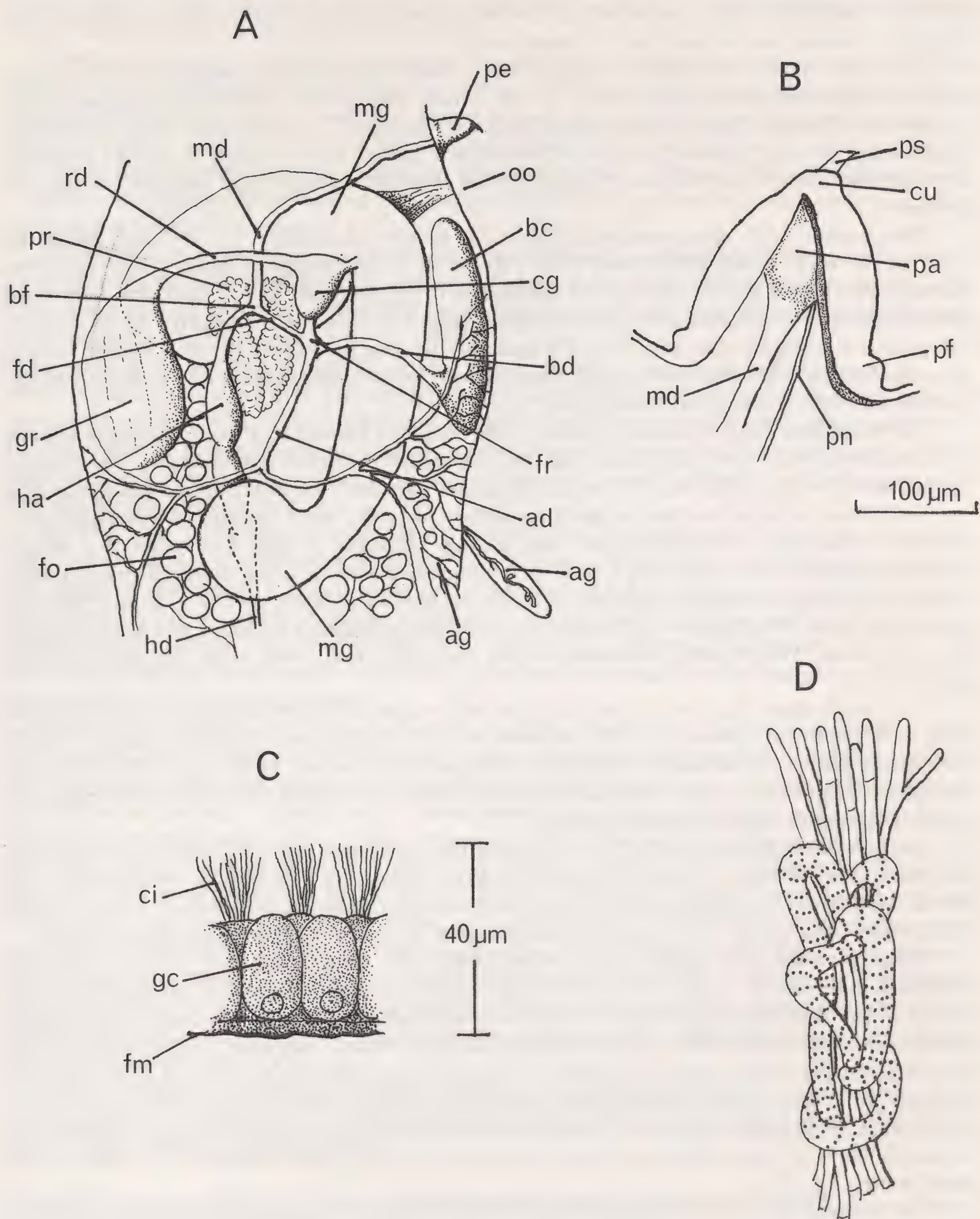


Fig. 3. A diagram of anterior genital region. The female duct from (bf) to (fr) has been displaced slightly for display purposes. B dissection sketch of penis. C cells of capsule gland wall. D egg ribbon. ad main albumen duct; ag albumen gland; bc bursa copulatrix; bd bursal duct; bf bifurcation of hermaphrodite duct; cg capsule gland; ci cilia; cu cupola; fd female duct; fm fibrous membrane; fo follicle of ovotestis; fr fertilization region; gc gland cell; gr genital receptacle; ha hermaphrodite ampulla; hd hermaphrodite duct; md male duct; mg mucous gland; oo oviducal opening; pa penial ampulla; pe penis; pf basal penial fold; pn penial nerve; pr prostate; ps penial style; rd receptacle duct.



follicles. The follicles are connected to the hermaphrodite duct which, after swelling to an ampulla, divides into a male and a female duct.

The male system is simple, it comprises the male duct, prostate, and penis. The female system is more elaborate and consists of the female duct with a fertilization region, bursa copulatrix, albumen gland, capsule gland, and mucous gland. Arrangements for the transfer of sperm vary. In some species the apex of the penis is armed with a hollow style, like a minute hypodermic needle, which is used to inject sperm through the body wall into the bursa of the partner.

The ovotestis of *P. viridis* consists of about 250 follicles of diameter 0.2–0.3 mm. Maturing ova line the wall of each follicle and files of sperm in various stages of development converge towards the central lumen. Most of the follicles lie in the posterior half of the body, with some pressed forward into the anterior genital region (Fig. 3A). They are connected by ductules to the median hermaphrodite duct (hd). On entering the anterior region, the duct widens to form an ampulla (ha) of three or four coils. It then narrows to its former diameter for a short distance, and divides into a male and female duct.

The male duct (md) is lined by ciliated cells; these are backed by a layer of spindle-shaped cells, followed by an outer coat of cuboidal cells bounded by an elastic membrane. The prostate (pr) is lobed; its duct enters near the beginning of the male duct. On entering the penis (Fig. 3B), the male duct enlarges to form a small ampulla (pa). The duct terminates externally in a cuticular style (ps) of length 40  $\mu\text{m}$  and average diameter 8  $\mu\text{m}$ . The penis is a simple outpushing of the body wall filled with loose connective tissue and a few muscle fibres. It has no strong attachment muscles to withdraw it inside the body. However, there is a circular fold (pf) around the base of the penis which allows it to sink inwards during deflation and form a boss on the body wall. When fully withdrawn it lies along the body wall with the style directed posteriorly.

The female duct (Fig. 3A, fd) begins at the bifurcation of the hermaphrodite duct (bf) and ends at the oviducal opening (oo). It commences with a short stretch that runs ventrally under the capsule gland. At the base of the gland the female duct is joined by the bursal duct (bd) and the main albumen duct (ad). The junction of these three ducts forms the fertilization region (fr) which enlarges during the female phase.

The tubular bursa copulatrix (bc) lies under the copulatory pad and is loosely attached to the body wall. In serial sections it contained sperm; some were attached by their heads to the bursal wall, most occupied the lumen, and a few were seen along the bursal duct. Lesions on the bursal wall next to the skin indicated where sperm had been injected during copulation.

The diffuse albumen gland (ag) ramifies along both sides of the body cavity. From the fertilization region the main albumen duct (ad) slants towards the median line and bifurcates dorsal to the stomach. Each branch serves one side and divides into tributaries with further subdivisions that closely follow those of the gut into the cerata. Trinchese (1873) was the first to demonstrate that the terminal branches were part of an albumen gland and he noted their presence in several other ascoglossans. This was a notable achievement. After leaving the fertilization region the female duct enters the capsule gland (cg). It has a lining of ciliated cells, a middle layer of large gland cells, and outer coat of thin cells bounded by a fibro-elastic membrane (Fig. 3C).

The receptacle duct (rd) begins at the left anterior corner of the capsule gland. It proceeds to the left, crossing dorsal to the oesophagus, and opens into the genital receptacle (gr) which is situated close to the left body wall, a position also occupied by the receptacles of *Costasiella liliana*e and *Hermaeina smithi*. The receptacle of *P. viridis* is large and ovoid (long axis, 4 mm). Its wall consists of three coats: an inner lining of cuboidal cells, a middle layer of gland cells, and an outer muscular coat. This is unusual, for the receptacles of most ascoglossan species have thin walls without a middle layer of gland cells. The receptacle of one specimen contained a large bolus which stained differentially with Masson's trichrome stain. One part consisted of sperm



which may have been swept out of the hermaphrodite ampulla at the beginning of a female phase; the other part was probably albumen.

The female duct leaves the right anterior corner of the capsule gland by a short section and enters the mucous gland at the point shown in Fig. 3A. The gland occupies about a third of the body cavity. It has an anterior and ventral part that is continued along the right side by a dorsal bridging section. The section curves towards the left and forms a large lobe. A mucous gland of this shape and volume is also possessed by *Placida dendritica*, *Hermaea bifida*, *H. variopicta* and *Caliphylla mediterranea*. After leaving the mucous gland, the female duct enters an atrium that leads to the oviducal opening.

An egg-ribbon of *P. viridis* was examined. It was about 5 mm long and 4.5 mm in diameter. It contained a tightly coiled string of evenly spaced capsules; their number was estimated to be 5000. Each capsule was of diameter 300  $\mu\text{m}$  and enclosed a yolky egg cell (diameter 120  $\mu\text{m}$ ) surrounded by clear albumen.

*Proposed mode of functioning.* In the male phase sperms pass from the ovotestis to the hermaphrodite ampulla where they are stored temporarily. Prior to copulation sperms pass into the male duct. Aided by ciliary action and contractions of the muscular wall of the male duct, and probably by prostatic secretion, they reach the penis. During copulation the style of one partner pierces the copulatory pad of the other, and sperms are injected into the bursa where they are stored until required.

In the female phase eggs accumulate in the ampulla. They then move into the fertilization region where they are fertilized and coated with albumen. From this region they pass into the capsule gland where each egg is encapsulated. They then enter the mucous gland. Here they are evenly spaced out on a mucoïd string, wrapped in another kind of mucus, and finally the egg-ribbon is given a sticky coat that enables it to adhere to a seaweed. The genital receptacle is probably a sump for sperm swept out of the hermaphrodite ampulla at the beginning of a female phase, and also for excess albumen.

*Comments.* Unfortunately we have not observed *P. viridis* copulating. The evidence in support of the proposed mode of functioning is therefore anatomical and comparative. *Limapontia capitata*, an ascoglossan common on the rocky shores of Northumberland, has a style similar in shape and dimensions to that of *P. viridis*, and a bursa copulatrix close to the body wall. It has been observed copulating many times. The partners lie head to tail with the style of one close to the bursa of the other. Though the bursal region is obscured, repeated stabs of the style in the bursal area of each animal are noted. When they separate, white flecks of sperm are sometimes seen, marking the positions of punctures. These and other evidences of hypodermic injection were described by Gascoigne (1956) for *Limapontia cocksi* and by Clark (1978) for *Stiliger fuscatus*. Functional and comparative anatomy suggest that the style of *P. viridis* is employed in the same manner. Adam and Leloup (1939) in a paper on *Alderia modesta*, were the first to note this novel method of sperm transference. It appears to be used by other stiligerids, though at present detailed observations are few.

On the female side the sequence of fertilization region, albumen gland, capsule gland, and mucous gland is a rational one. Studies of animals in the female phase are needed to trace the path of eggs along the mucous gland.

*Central Nervous System* (Fig. 4). The cerebral ganglia sit like a saddle on the oesophagus and are connected to the pedal ganglia, forming the nerve ring. The buccal ganglia lie in the angle formed by the junction of the oesophagus with the buccal mass. They are linked to the nerve ring by two cerebrobuccal connectives; each joins the cerebral ganglion on the same side, low down on its anterior, or inner, face. B1 runs forward into the buccal musculature; bla is a small nerve to the salivary reservoir. Stomato-gastric nerves (stg) run down the sides of the oesophagus to the stomach. On the right cerebral ganglion of Fig. 4, the forwardly-directed nerves are displayed: c1 to the tentacle; c2 to the velum and oral tube; c3 to the dorsal part of the



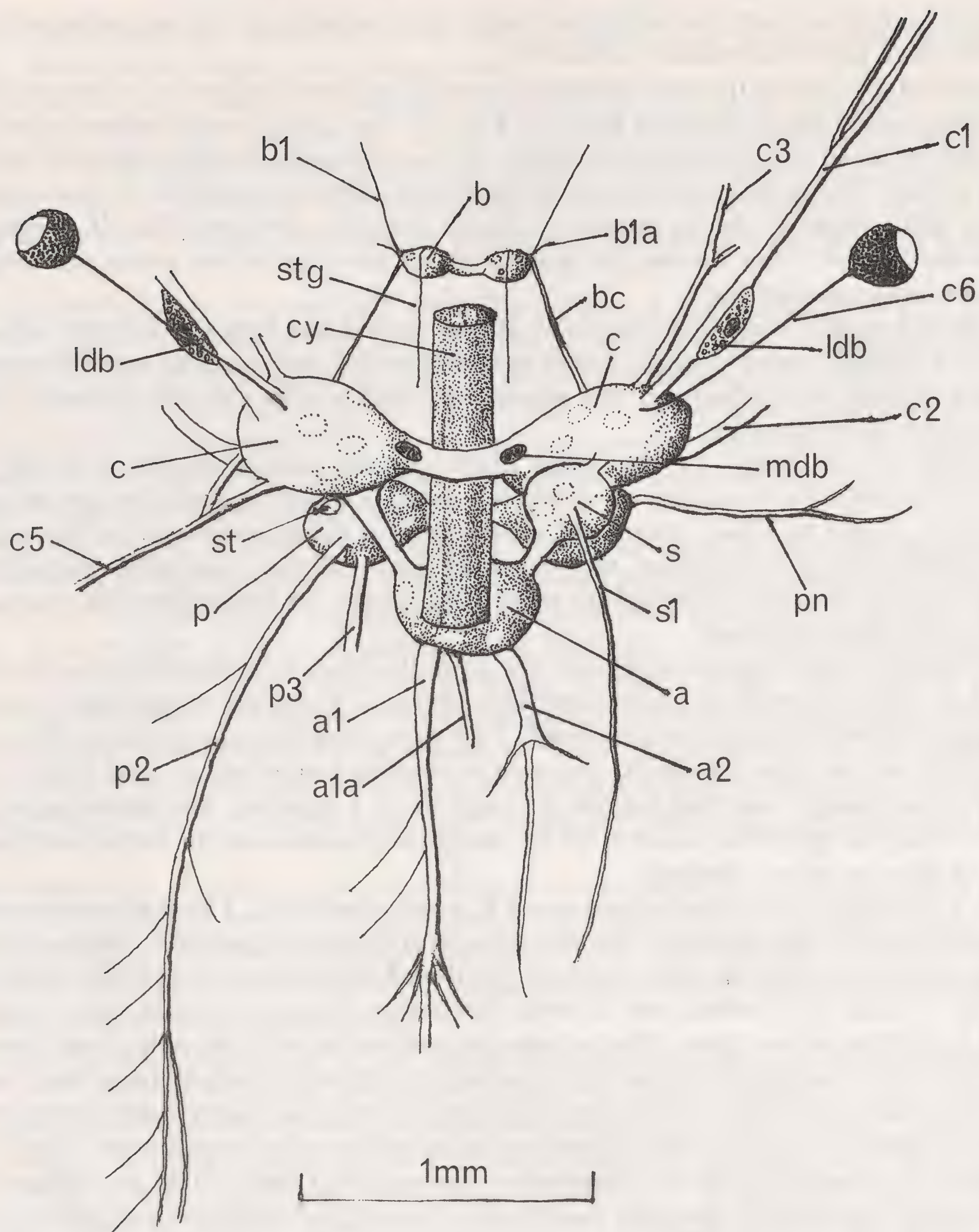


Fig. 4. Diagram of central nervous system. In order to simplify the figure c5, p2, p3 are not shown on the right. Cy is a cylinder representing the part of the oesophagus that passes through the nerve ring and above the visceral loop. a abdominal ganglion; a1, a1a, a2 abdominal nerves; b buccal ganglion; bc cerebrobuccal connective; b1, b1a, stg buccal nerves; c cerebral ganglion; c1, c2, c3, c5, c6 cerebral nerves; cy cylinder; ldb latero-dorsal body; mdb medio-dorsal body; p pedal ganglion; pn penial nerve; p2, p3 pedal nerves; s supra-intestinal ganglion; sl supra-intestinal nerve; st statocyst; stg stomato-gastric nerve.

head; and c6, the optic nerve. On the left cerebral ganglion c5 is depicted – it innervates a group of anterior cerata. The penial nerve (pn) runs directly from the right pedal ganglion to near the apex of the penis; and on the way gives off a branch to the body wall. On the left pedal nerve p2 is shown; it runs along the side of the body below the cerata and innervates most of them. P1 and p3 are typical of most ascoglossans and serve the muscles of the foot in the anterior and posterior regions.

*Placida viridis* is one of the few shell-less ascoglossans in which the visceral loop connectives are visible, the cerebro-abdominal being the longest. The shape of the loop is characteristic of *P.*



*viridis* and *P. dendritica*. The abdominal ganglion has three nerves A1 runs to the stomach where it spreads out in fine branches; ala is a minor nerve that ends on the ventral surface of the oesophagus. A2 is a genital nerve, sending branches to the hermaphrodite ampulla and to the point of bifurcation (Fig. 3A. bf) and a branch runs ventrally near the median line into the posterior region of the ovotestis. The supra-intestinal ganglion has only one nerve (sl) which was traced as far as the renal swelling.

Two medio-dorsal bodies (mdb) are present in *P. viridis*; one at each end of the cerebral commissure. Each consists of two neurons enclosed in a capsule. Similar bodies have been found in 12 other ascoglossan species. A swelling (ldb) is present near the base of cl; it consists of a cluster of small neurons and a large one, encased in a thin membrane. This has been termed a rhinophoral ganglion, though the swelling is not typically ganglionic. It resembles more the latero-dorsal bodies present in *Lymnaea stagnalis*. We have therefore preferred tentatively to call the cluster a latero-dorsal body. A statocyst (st) lies on the anterior border of each pedal ganglion.

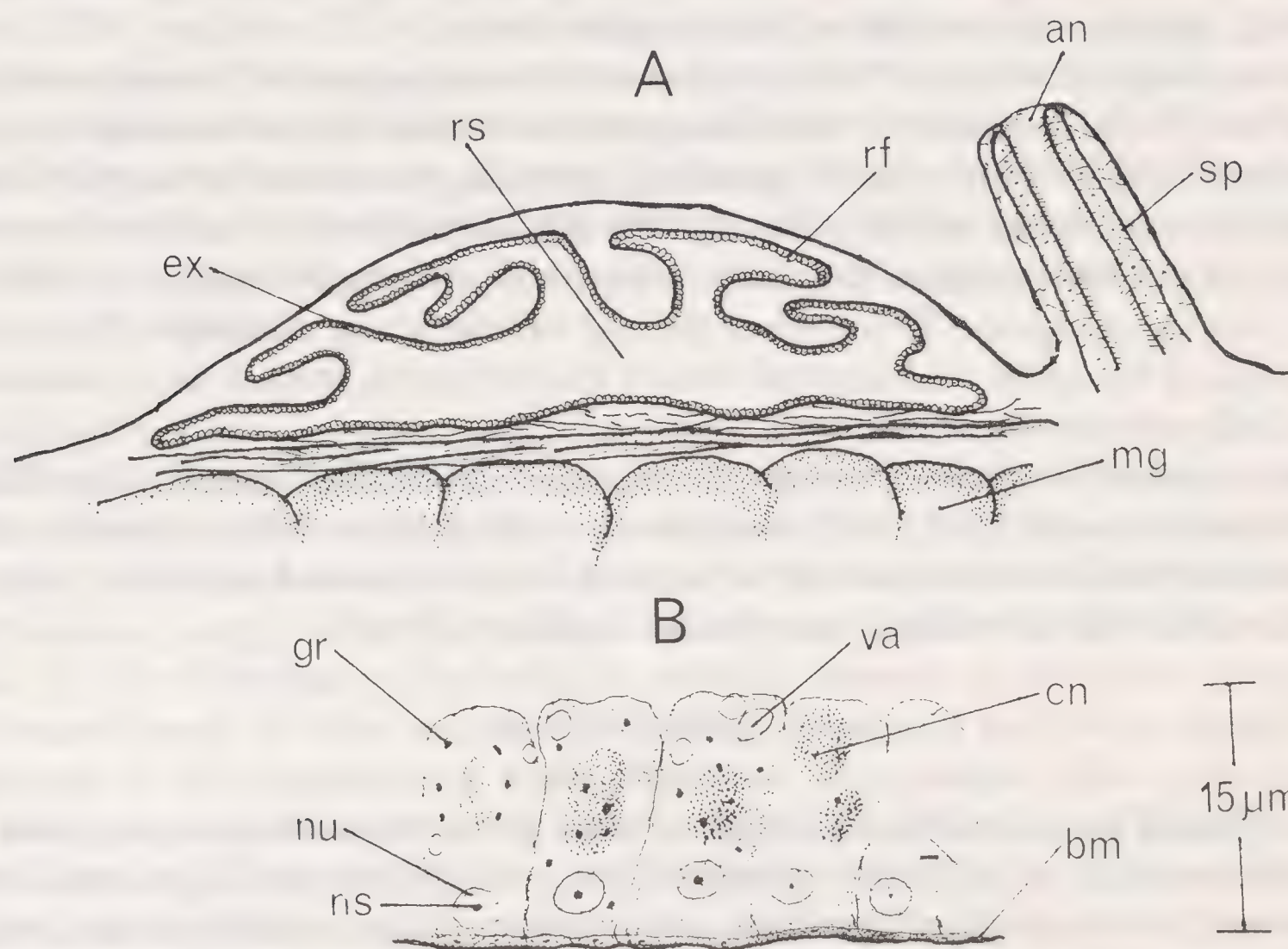


Fig. 5. A median section of renal swelling (diagrammatic). B an assemblage of excretory cells. They were drawn from paraffin sections prepared by R. D. Manuel. The specimen was preserved in Bouin's fluid; sections were cut at 10 μm and stained by Masson's trichrome method.

an anus; bm elastic membrane; cn concretion; ec excretory cell; gr granule; mg mucous gland; ns nucleolus; nu nucleus; rf renal fold; rs renal sac; sp anal spout; va vacuole.

**Comments.** The length of the visceral loop in *P. viridis* is probably not a primitive feature for it bears only two ganglia. Its length could be due to local topography or developmental conditions. Note that the ceratal innervation does not imply a pedal or cephalic origin of cerata.

**Heart and Kidney.** In nearly all ascoglossans, the heart lies in the anterior half of the body, just beneath the dorsal surface. It consists of a muscular ventricle and a thin walled auricle. The kidney is a conical sac, posterior to the heart. These two organs lie close together forming a reno-pericardial swelling. The renal region appears whitish, granular, and crystalline, and the anterior pericardial region can plainly be seen pulsating in living animals.

In *Placida dendritica* the heart contracts rapidly and relaxes slowly, and the pulse rate is about 60 min<sup>-1</sup>. *Placida viridis* is exceptional. The entire dorsal swelling appears granular and crystalline. No heart beat can be discerned in the anterior region. The entire swelling pulsates



slowly (about  $30 \text{ min}^{-1}$ ) commencing posteriorly and travelling forwards. This could be caused by muscle fibres in the wall of the swelling and nearby.

It was easy to show, by fine dissection, that *P. dendritica* has a heart; but repeated dissections of *P. viridis* failed to find a heart in, or near, the dorsal swelling. Transverse, horizontal, and sagittal serial sections prepared by M. Sordi, and an additional series by R. Manuel, confirmed that *P. viridis* does not possess a heart.

The renal sac is ovoid (long axis about 2 mm) and, as Fig. 5A shows, it occupies most of the dorsal swelling. The surface area of the sac is increased by outfolds over the dorsal and lateral sides; the folds run mostly lengthwise, occasionally ramifying and joining. Excretory cells line the renal sac and its folds; they are attached by their bases to a thin layer of cells bounded by a membrane. Fig. 5B illustrates a collection of excretory cells; their details correspond fairly well to those described by Fretter and Graham (1962) for prosobranchs. Each excretory cell (length 10–15  $\mu\text{m}$ ) has a basal nucleus with a nucleolus; the cytoplasm may include several small granules, a concretion, large or small vacuoles. The renal pore opens on the anterior third of the renal swelling, slightly to the right of the median line.

*Comments.* It seems possible that *P. viridis* has a circulation promoted by contractions of muscle fibres in the body wall and aided by movements of the cerata. Any flow round the cerata would not be impeded by lateral branches of gastric diverticula, such as are present in the cerata of *P. dendritica*. Respiration could be effected across the skin of the slender body and numerous cerata. Since no part of the body is more than 2 mm from the surface, diffusion, assisted by muscular movement, may be adequate. Branches of the gut extend along the sides of the body, over the renal swelling and the penis, and into the cerata and tentacles, so that the products of digestion have but a little way to travel.

Trinchese made no reference to the absence of a heart in *P. viridis*. He called the renal swelling a hydrocardium (1873) and noted that it contained excretory granules (1893). Evans (1953) established by dissection and serial sections that *Alderia modesta* has no heart; and, as far as we know, this is the only other ascoglossan lacking a heart.

## DISCUSSION

*Comparison of Placida viridis and Hermaea bifida.* At first glance the two species appear to be closely related. Both are of the same length (about 15 mm), are slender in shape, and have numerous fusiform cerata. Each has a dorsal swelling, and anterior to this, a median anal spout. Each has a male and a female opening on the right side. The female openings differ in function. During copulation the tentaculiform penis of *H. bifida* is thrust through the female opening and sperm travel along the female duct, eventually reaching the bursa copulatrix. Towards the close of a female phase the egg-ribbon is passed out of the female opening. Thus it serves in turn as a vaginal and an oviducal opening. In *P. viridis* the penis does not pass through the female opening. During copulation sperm are injected through the body wall into the bursa by the cuticular style. The female opening serves only for the passage of the egg-ribbon and is more precisely called an oviducal opening.

*H. bifida* lacks the dark violet pigment of *P. viridis* and the two stripes along the sole of the foot. The gut of *H. bifida* has a rosy tinge because it feeds on the pale to bright crimson sap of *Griffithsia corallinoides*; whereas the gut of *P. viridis* is greenish since it feeds on *Bryopsis*. A copulatory pad can be seen on the right side of *P. viridis*. This swelling is not present in *H. bifida*.

Internally the two species differ markedly. *H. bifida* has a well-developed heart; *P. viridis* lacks a heart. They differ in general plan and details of the reproductive system. *H. bifida* is diaulic; *P. viridis* is pseudo-diaulic. The follicles of the ovotestis of *H. bifida* are large and lobulated, in number about 80; those of *P. viridis* are spherical and numerous (about 250). The prostate of *H. bifida* is compact; that of *P. viridis* is lobed. *H. bifida* has a tentacular penis of length 3 mm and has no style; the penis of *P. viridis* is conical, about 0.5 mm long, and is surmounted by



a short cuticular style. The bursa copulatrix of *H. bifida* is small, spherical, and lies deep within the anterior genital complex. The bursa of *P. viridis* is large, elongated and lies close to the body wall on the right side. The genital receptacle of *P. viridis* lies next to the body wall on the left; that of *H. bifida* is situated anteriorly near the median line. The albumen gland of *P. viridis* terminates in lobules inside the cerata; in *H. bifida* the gland ends in thick-walled capsules that do not appear in the cerata. The arrangement of ducts around the fertilization region in *H. bifida* is less concentrated than in *P. viridis*. The capsule gland of *H. bifida* is tubular and continued by a long stretch of female duct; in *P. viridis* the gland is ovoid and is connected to the mucous gland by a shorter length of female duct.

In *H. bifida* the gastric trunks are continued by two, long lateral diverticula, one each side, from which the ceratal diverticula arise; this is a common pattern in ascoglossans. In *P. viridis* (and *P. dendritica*) long lateral diverticula are not present. The stomach of *P. viridis* differs from that of *H. bifida* in having a median typhlosole-like fold. The oesophageal pouch of *H. bifida* lies well forward, ventral to the buccal mass.

Pelseneer (1894) regarded *H. bifida* as having 3 ganglia on the visceral loop, but dissections of specimens from Carna, Ireland, showed it has only two. On the other hand, *Hermaea variopicta*, a more primitive species than *H. bifida*, has three ganglia on the visceral loop (Gascoigne, 1979). *Hermaea* can be regarded as showing a transition from three to two visceral loop ganglia, or having constantly three. *P. viridis* has only two ganglia on the visceral loop, like all other stiligerids. Its loop is longer than that of *H. bifida*; and medio-dorsal bodies are present in *P. viridis* but not in *H. bifida*.

*Systematic position of H. bifida, P. viridis, and P. dendritica.* The differences noted in the text between *P. viridis* and *P. dendritica* are of importance, for it was formerly thought the species differed only in a few external features (Pruvot-Fol, 1954; Gascoigne, 1976) and this may have led to doubts about the validity of *P. viridis* as a species. The many differences noted above between *H. bifida* and *P. viridis* lead one to suppose that the two species are not as closely related as some authors would have us think. In the following paragraphs an attempt is made to group the two genera into families in a natural way. For this taxonomic exercise characters have been sought that might indicate changes of an evolutionary kind. Shell-less ascoglossans show two main trends. The central nervous system becomes more concentrated by a shortening of the visceral loop and a reduction of its ganglia from three to two. The reproductive system changes from diaulic to pseudo-diaulic and the penial style becomes an instrument used in a new method of sperm transference.

Gascoigne (1979) suggested that penetrant styles evolved in diaulic ancestors during a period of time when the bursa moved towards the body wall and other changes took place that are characteristic of a pseudo-diaulic system. Some of these changes are illustrated by the comparison of *H. bifida* with *P. viridis*. The central nervous system also evolved by the disappearance of the sub-intestinal ganglion. Using these characters, shell-less species may be regrouped as in the following schema (see p. 178), based on one by Gascoigne (1976) that was improved by Baba (personal communication).

The many genera in Group 2 suggest that their penial styles evolved recently, probably in the Eocene, and since then most of the ancestral species have disappeared. It may be that in the family Caliphyllidae the ancestral condition is represented by *Caliphylla* and a style appears as a new development in the genus *Cyerce*. A few species in Group 2 (for example *Ercolania margaritae*) show an advance on pseudo-diauly. The bursa, which lies close to the body wall, acquires a short duct to the exterior. The reproductive system is now triaulic, and the penis retains its style. As far as *Placida* and *Hermaea* are concerned they may be regarded as separate genera in different groupings of families for the reasons given above.

The acardiac condition of *P. viridis* may raise some doubts. It could be placed in the family Alderiidae, because *Alderia modesta* lacks a heart, is pseudo-diaulic and has two ganglia on the



## GROUP 1

|        |                                                 |
|--------|-------------------------------------------------|
|        | Usually without a penial<br>style often diaulic |
|        | 3 ganglia on the visceral loop                  |
| Family | CALIPHYLLIDAE                                   |
|        | <i>Caliphylla</i>                               |
|        | <i>Polybranchia</i>                             |
|        | <i>Cyerce</i>                                   |
| Family | HERMAEIDAE                                      |
|        | <i>Hermaea</i>                                  |

## GROUP 2

|            |                                                     |
|------------|-----------------------------------------------------|
|            | Always with a penial style<br>mostly pseudo-diaulic |
|            | 2 ganglia on the visceral loop                      |
| Family     | STILIGERIDAE                                        |
| Sub-family | STILIGERINAE                                        |
|            | <i>Stiliger</i>                                     |
|            | <i>Ercolania</i>                                    |
|            | <i>Olea</i>                                         |
|            | <i>Calliopaea</i>                                   |
|            | <i>Alderiopsis</i>                                  |
|            | <i>Placida</i>                                      |
| Sub-family | LIMAPONTIINAE                                       |
|            | <i>Limapontia</i>                                   |
| Family     | ALDERIIDAE                                          |
|            | <i>Alderia</i>                                      |

visceral loop. However, the pseudo-diauly of *A. modesta* has many unusual features. The follicles have no ductules; the capsule gland, if present, is not a distinct organ; the mucous gland does not resemble that of *P. viridis*; the bursa is situated at some distance from the body wall and the penetrant style is long and has numerous spinules. The visceral loop is shorter and not of the same shape as that of *P. viridis*. The adult tooth of *A. modesta* is characteristic of the species and unlike the awl-shaped tooth of *P. viridis*. Many external features differ from those of *P. viridis*. From these considerations it seems better to leave the genus *Placida* in the family Stiligeridae.

*Placida dendritica* has a heart, and some details of its female system (so brilliantly described by Pelseneer, 1894) bear little resemblance to those of *P. viridis*. On the other hand, it possesses a penetrant style and copulatory pad like those of *P. viridis*; its central nervous system is almost an exact copy of that of *P. viridis*; and the two species resemble one another closely in external features. We suggest that *P. dendritica* remains in the genus *Placida*.

## ADDENDUM

When studying *P. viridis* we were attracted by the similarity of its radula and teeth to those of some other species. The observations are appended because they emphasize the point that the first few elements, formed before the appearance of the first fully-formed tooth, are worthy of further study.

*Comparison of radulae.* Both *H. bifida* and *P. viridis* have awl-shaped teeth and all elements are retained on the radular ribbon. Radulae of the two genera can be arranged in a series (Table 1) that illustrates progressive reduction in the number of elements.

TABLE 1

| Species                   | Rudiments | Transitional<br>teeth | Position<br>of first adult<br>tooth | Approx. No.<br>of adult teeth |
|---------------------------|-----------|-----------------------|-------------------------------------|-------------------------------|
| <i>Hermaea variopicta</i> | 6         | 6                     | E13                                 | 60                            |
| <i>H. bifida</i>          | 6         | 3                     | E10                                 | 60                            |
| <i>Placida dendritica</i> | 6         | 1                     | E8                                  | 40                            |
| <i>P. viridis</i>         | 2         | 1                     | E4                                  | 30                            |

If the animal is small, or poorly preserved, Table 1 may serve as a minor aid to identification. However small the specimen, it could be distinguished by the position of the first tooth. The numbers given in the table are fairly constant as far as rudiments and transitional teeth are concerned. For example, Trinchese (1877) published a drawing of the radula of *P.*



*dendritica*. He described the first five elements as 'senza cuspidè'; two transitional teeth are discernible; and E7, or E8 is the first adult tooth.

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# THE MOLLUSCA OF ACID WOODLAND IN THE ITALIAN PROVINCE OF NOVARA

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*Abstract:* A rich fauna of 55 species of terrestrial molluscs was obtained from 14 sites in acidic woodland (pH range 3.8-5.3) in the southern Alps. The flora and fauna of the sites were investigated using principal coordinates analysis, and the interpretation of some of the major directions of variation was possible. In overall terms however, vegetation and soil pH proved to be poor at accounting for variations in the snail fauna.

Snails are generally more abundant on soils which are neutral or basic (pH 6.5 or above). There are relatively few studies devoted specifically to the mollusc faunas of woodland on acidic soils, amongst which may be mentioned Bishop (1977a) on south-west Ireland, and Wäreborn (1969) on southern Sweden. It was therefore considered of interest to examine woodland sites on acidic soils in southern Europe, the area chosen for study being in the southern Alps.

Ideas about the relationships of snails to their environment run through a wide spectrum of alternatives. At one extreme is the view that the snails themselves form distinct communities, or that there exist characteristic snail assemblages associated with particular plant communities or soil types. At the other extreme is the view that each snail species behaves quite independently of all others, and that its individual distribution may be related solely to environmental factors, the vagaries of site history, or dispersal mechanisms.

Whilst the author is more sympathetic with the latter view, it was pointed out (Bishop 1977b) that a quantitative approach to habitat surveys might be a rapid way of providing ideas for more detailed testing. This suggestion was taken up in studies in Somerset (Bishop, 1976a), and in south-west Ireland (Bishop, 1977a), when it became apparent that strong correlations between factors which had often been singled out, *a priori*, by previous workers could lead to difficulty in causal interpretation.

The present study illustrates the considerable diversity of snails and slugs in acidic woodland on the southern side of the Alps in the province of Novara, Italy.

## METHODS

Fourteen sample sites, each of size 10 × 10 m, were selected in June 1975 on the basis of their vegetation. These were chosen to be uniform within themselves, without obvious environmental or vegetational change. A sample was obtained from the top 50 mm of soil at each site, and the pH determined electrometrically in 1:2.5 suspension (by volume) with distilled water. A description of the vegetation was prepared for each site, and samples taken for later identification where necessary. The mollusc fauna was sampled by sieving litter and top soil through a 10 mm sieve. A hand search was made for slugs and the larger snails, lifting fallen logs and stones and investigating crevices and the bark of trees. In the laboratory, the sieve samples were separated into three fractions by the use of 2.5 and 0.6 mm sieves. Each fraction was examined under a binocular microscope, and the live molluscs were identified.





Fig. 1. A map showing the location of the fourteen study sites A–N in the province of Novara, Italy.

## RESULTS

*The Study Sites.* The location of the 14 sites, A–N, is shown in Fig. 1. These are situated in the prealps (A, B, G, E, F, N), or along alpine valleys (C, D, H, I, J, K, L, M), in the province of Novara, Italy. All are in woodland, the prealpine zone being heavily exploited, with regular coppicing of the chestnut woods. The woods of the higher part of the alpine zone are of larch and spruce, and are less disturbed by the activities of man.

Site A is at Sotto Germagno, Valstrona (Universal Transverse Mercator Grid Reference MR5282), at a height of 400 m above sea-level. Soil pH 4.0.

Site B is at Fornero, Valstrona (MR4884), at a height of 500 m. Soil pH 4.8.

Site C is at Boschetto, Val di Antrona (MS4102), at a height of 450 m. Soil pH 4.4.

Site D is at Viganella, Val di Antrona (MS3800), at a height of 550 m. Soil pH 4.7.

Site E is at Armeno, above Lago d'Orta (MR5877), at a height of 500 m. Soil pH 3.6.

Site F is at Arola, Lago d'Orta (MR5175), at a height of 500 m. Soil pH 3.8.

Site G is at Bolzano Novara, Lago d'Orta (MR5769), at a height of 350 m. Soil pH 3.7.

Site H is at Pecetto, Valle Anzasca (MR1992), at a height of 1350 m. Soil pH 4.3.

Site I is at Macugnaga, Valle Anzasca (MR2192), at a height of 1250 m. Soil pH 4.9.

Site J is at Prequatera, Valle Anzasca (MR2891), at a height of 750 m. Soil pH 4.8.

Site K is at Schieranco, Val di Antrona (MS3200), at a height of 800 m. Soil pH 3.9.

Site L is at Pieve Vergonte, Val d'Ossola (MR4494), at a height of 220 m. Soil pH 5.3.

Site M is at Gozzi, Valle Anzasca (MR4197), at a height of 400 m. Soil pH 4.8.

Site N is at Gignese, Lago Maggiore (MR6278), at a height of 650 m. Soil pH 4.1.

Soils are developed on base-poor mica schists. There is no significant correlation between altitude and pH (Spearman's rank order correlation coefficient  $r_s = 0.038$ , probability  $p = 0.45$ ).



# THE MOLLUSCA OF ACID WOODLAND

*The Vegetation.* The vegetation of the fourteen sites is summarized in Table 1. The recorded vascular flora consists of 101 species, and the bryophyte flora of 52 species. Species found at only one site were eliminated, and a table of similarities was constructed for each pair of sites in terms of distances, such that the least similar sites were placed farthest apart. After elimination of plants of unique occurrence there remained 64 vascular plants and 16 bryophytes. It would require axes in fourteen dimensions to represent fully the distances between sites, and data reduction was performed by principal coordinates analysis (Blackith and Reyment, 1971) to represent the distances in fewer dimensions. Three axes could represent 46% of the total variance between sites for vascular plants and 57% for bryophytes.

For vascular plants, the scores on axis 1 were correlated with altitude ( $r_s = 0.52$ ,  $p = 0.03$ ). *Acer pseudoplatanus* and *Anemone nemorosa* were more frequent in the higher woods and *Athyrium filix-femina*, *Geranium robertianum* and *Hedera helix* were more frequent in the lower woods. The scores on axis 3 were correlated with pH ( $r_s = 0.61$ ,  $p = 0.01$ ). *Castanea sativa* and *Viola riviniana* were more frequent in the acidic woods and *Dactylis glomerata*, *Fraxinus excelsior*, and *Phyteuma spicata* were more frequent in the less acidic woods.

The first three axes for bryophytes could not be interpreted, due to the very sparse occurrence of the different species of this group. However, there was some indication that vascular plants and bryophytes were behaving in a similar manner. The first axis scores for bryophytes were correlated with the first axis scores for plants (Pearson's product moment correlation coefficient  $r_p = 0.47$ ,  $p = 0.05$ ), and the second axis scores for bryophytes were correlated with the second axis scores for plants ( $r_p = 0.52$ ,  $p = 0.03$ ).

TABLE 1

The flora of the fourteen sites in acid woodland in the province of Novara, Italy

| VASCULAR PLANTS                               | SITES |   |   |   |   |   |   |   |   |   |   |   |   |   |
|-----------------------------------------------|-------|---|---|---|---|---|---|---|---|---|---|---|---|---|
|                                               | A     | B | C | D | E | F | G | H | I | J | K | L | M | N |
| <i>Acer campestre</i> L.                      | +     | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>A. pseudoplatanus</i> L.                   | .     | . | . | . | . | . | . | + | + | + | . | . | . | . |
| <i>Actaea spicata</i> L.                      | .     | . | . | . | . | . | . | . | + | . | . | . | . | . |
| <i>Allium ursinum</i> L.                      | .     | . | + | + | . | . | . | . | . | . | . | . | . | . |
| <i>Alnus glutinosa</i> (L.) Gaertn.           | .     | . | . | + | . | . | . | . | . | . | . | . | . | . |
| <i>A. incana</i> (L.) Moench.                 | .     | . | . | . | . | . | . | + | . | . | . | . | . | + |
| <i>Anemone nemorosa</i> L.                    | .     | . | + | . | . | + | + | + | . | + | + | . | . | . |
| <i>Angelica sylvestris</i> L.                 | .     | . | . | . | . | . | . | . | + | . | . | . | . | . |
| <i>Anthoxanthemum odoratum</i> L.             | .     | . | + | + | . | . | . | . | . | . | . | . | . | . |
| <i>Aruncus dioicus</i> (Walter) Fernald       | +     | + | . | + | . | . | . | . | . | . | + | + | + | + |
| <i>Asarum europeum</i> L.                     | +     | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Asperula taurina</i> L.                    | .     | + | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Asplenium tichomanes</i> L.                | .     | + | + | + | . | . | . | . | . | + | + | . | . | . |
| <i>Astrantia major</i> L.                     | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>Athyrium filix-femina</i> (L.) Roth        | +     | + | + | + | . | . | . | . | . | . | . | + | . | + |
| <i>Brachypodium sylvaticum</i> (Huds.) Beauv. | .     | + | + | + | + | . | . | . | . | . | . | . | . | . |
| <i>Castanea sativa</i> Mill.                  | +     | + | + | . | + | + | + | . | . | + | . | . | + | + |
| <i>Calluna vulgaris</i> (L.) Hull             | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>Cardaminopsis halleri</i> (L.) Hayek       | +     | . | . | . | . | . | . | . | + | . | . | . | . | . |
| <i>Chamaecystis purpureus</i> (Scop.) Link    | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>Coronilla emerus</i> L.                    | .     | + | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Coryllus avellana</i> L.                   | +     | + | + | + | + | + | + | . | + | + | + | + | + | + |
| <i>Chelidonium majus</i> L.                   | .     | . | . | . | . | . | . | . | . | . | . | + | . | . |
| <i>Crataegus monogyna</i> Jacq.               | +     | . | . | . | . | + | . | . | . | . | . | . | . | . |
| <i>Cyclamen hederifolium</i> Aiton            | .     | + | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>Dactylis glomerata</i> L.                  | .     | . | + | + | . | . | . | . | . | . | . | + | . | + |
| <i>Dactylorhiza fuchsii</i> (Druce) Soo       | .     | . | + | . | . | . | . | . | + | . | . | . | . | . |



| VASCULAR PLANTS                                | SITES |   |   |   |   |   |   |   |   |   |   |   |   |   |
|------------------------------------------------|-------|---|---|---|---|---|---|---|---|---|---|---|---|---|
|                                                | A     | B | C | D | E | F | G | H | I | J | K | L | M | N |
| <i>D. sambucina</i> (L.) Soo                   | .     | . | . | . | . | . | . | . | + | . | . | . | . | . |
| <i>Daphne laureola</i> L.                      | .     | . | . | . | . | . | . | . | . | . | + | . | . | . |
| <i>Dryopteris filix-mas</i> (L.) Schott        | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>D. pseudomas</i> (Wollaston) Holub & Pouzar | +     | . | . | . | + | . | . | . | + | + | + | + | + | . |
| <i>Euonymus europaeus</i> L.                   | +     | . | . | + | . | . | . | . | . | . | . | + | . | . |
| <i>Eupatorium cannabinum</i> L.                | .     | . | . | + | . | . | . | . | . | . | . | . | . | . |
| <i>Euphorbia carniolica</i> Jacq.              | +     | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>E. cyparissias</i> L.                       | .     | . | . | . | . | . | . | . | + | . | . | . | . | . |
| <i>E. epithymoides</i> L.                      | .     | + | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>Fagus sylvatica</i> L.                      | .     | . | . | . | . | . | . | . | + | . | . | . | . | + |
| <i>Fragaria vesca</i> L.                       | .     | . | + | + | . | . | . | . | . | . | + | . | . | . |
| <i>Fraxinus excelsior</i> L.                   | .     | + | + | + | + | . | . | . | + | + | + | + | + | + |
| <i>Galeobdolon luteum</i> Huds.                | +     | + | . | . | + | . | . | . | . | + | . | . | + | . |
| <i>Galium odoratum</i> (L.) Scop.              | +     | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Genista germanica</i> L.                    | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>Geranium robertianum</i> L.                 | +     | + | + | + | . | . | . | . | . | + | . | + | + | . |
| <i>G. sylvaticum</i> L.                        | .     | . | . | . | . | . | . | . | + | + | + | . | . | . |
| <i>Geum urbanum</i> L.                         | .     | . | . | . | . | . | . | . | . | . | . | + | . | . |
| <i>Hedera helix</i> L.                         | +     | + | + | + | . | . | . | . | . | . | . | + | + | . |
| <i>Hepatica nobilis</i> Mill.                  | +     | + | + | . | . | + | . | . | . | . | + | . | . | . |
| <i>Hieracium argillaceum</i> Jordan            | .     | + | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>H. murorum</i> L.                           | .     | . | + | . | . | . | . | . | . | . | + | . | . | . |
| <i>Larix decidua</i> Mill.                     | .     | . | . | . | . | . | . | + | + | . | . | . | . | + |
| <i>Lathyrus niger</i> (L.) Bernh.              | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>Luzula nivea</i> (L.) D.C.                  | +     | + | . | + | + | . | . | . | + | . | + | + | + | + |
| <i>L. pilosa</i> (L.) Willd.                   | +     | + | . | + | . | . | + | . | . | . | . | . | . | . |
| <i>L. sylvatica</i> (Huds.) Gaud.              | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>Lysimachia memorum</i> L.                   | .     | . | . | + | + | . | . | . | . | . | . | . | . | + |
| <i>Maianthemum bifolium</i> (L.) Schmidt       | .     | . | . | . | . | . | + | + | + | . | . | . | . | . |
| <i>Melica nutans</i> L.                        | .     | . | + | . | . | + | . | . | . | . | + | + | . | . |
| <i>Mercurialis perennis</i> L.                 | +     | . | . | . | . | + | . | . | . | . | . | . | . | . |
| <i>Oxalis acetosella</i> L.                    | .     | . | + | . | + | . | . | . | . | + | + | . | . | + |
| <i>Paris quadrifolia</i> L.                    | .     | . | . | . | . | . | . | . | + | . | . | . | . | + |
| <i>Petastites hybridus</i> (L.) Gaertn.        | +     | . | . | . | + | . | . | . | . | . | + | . | . | + |
| <i>Phyllitis scolopendrium</i> (L.) Newm.      | .     | . | . | . | . | . | . | . | . | . | . | . | + | . |
| <i>Phyteuma spicata</i> L.                     | .     | + | + | + | . | . | . | . | + | + | . | + | + | . |
| <i>Polygonatum odoratum</i> (Mill.) Druce      | +     | . | . | . | . | . | + | . | . | . | . | + | . | . |
| <i>Poa trivialis</i> L.                        | +     | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Polypodium vulgare</i> L.                   | .     | . | . | . | + | . | . | + | . | . | . | . | . | . |
| <i>Populus tremula</i> L.                      | .     | . | . | . | . | . | . | + | . | . | . | . | . | . |
| <i>Potentilla erecta</i> (L.) Rausch           | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>Primula vulgaris</i> Huds.                  | +     | + | + | + | . | + | . | . | . | . | . | . | . | + |
| <i>Prunus padus</i> L.                         | .     | . | . | . | . | . | + | . | . | . | . | . | . | . |
| <i>Pteridium aquilinum</i> (L.) Kuhn.          | .     | . | + | . | . | + | + | . | . | . | . | . | . | . |
| <i>Pulmonaria officinalis</i> L.               | +     | + | . | . | . | . | . | . | . | . | + | + | . | . |
| <i>Ranunculus acris</i> L.                     | +     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>R. platanifolius</i> L.                     | +     | + | + | . | + | . | . | . | + | . | . | . | . | . |
| <i>Rhododendron ferrugineum</i> L.             | .     | . | . | . | . | . | . | + | . | . | . | . | . | . |
| <i>Robinia pseudacacia</i> L.                  | .     | . | . | . | . | . | . | + | . | . | . | + | . | . |
| <i>Rubus idaeus</i> L.                         | .     | . | . | . | . | . | . | . | + | . | . | . | . | . |
| <i>Rubus fruticosus</i> L. agg.                | +     | + | + | + | + | + | + | . | . | + | + | + | + | + |
| <i>Ruscus aculeatus</i> L.                     | +     | . | . | . | . | . | . | . | . | . | . | . | + | . |
| <i>Sambucus niger</i> L.                       | .     | . | . | . | . | . | . | . | . | . | . | + | + | . |
| <i>S. racemosus</i> L.                         | +     | . | . | . | + | . | . | . | . | + | . | . | . | . |
| <i>Sarothamnus scoparius</i> (L.) Wimmer       | .     | . | + | . | . | + | . | . | . | . | . | . | . | . |
| <i>Scrophularia nodosa</i> L.                  | .     | . | . | + | . | . | . | . | . | . | . | + | . | . |
| <i>Silene dioica</i> (L.) Clairv.              | +     | + | . | . | . | . | . | . | + | + | . | . | . | . |
| <i>S. vulgaris</i> (Moench) Garcke             | .     | + | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Sorbus aucuparia</i> L.                     | .     | . | . | . | . | . | . | . | + | + | + | . | . | . |



# THE MOLLUSCA OF ACID WOODLAND

|                                                             | SITES |   |   |   |   |   |   |   |   |   |   |   |   |   |
|-------------------------------------------------------------|-------|---|---|---|---|---|---|---|---|---|---|---|---|---|
|                                                             | A     | B | C | D | E | F | G | H | I | J | K | L | M | N |
| VASCULAR PLANTS                                             |       |   |   |   |   |   |   |   |   |   |   |   |   |   |
| <i>Stellaria nemorum</i> L.                                 | +     | . | . | . | + | . | . | . | . | . | . | . | . | . |
| <i>Tamus communis</i> L.                                    | .     | + | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Teucrium scorodonia</i> L.                               | .     | . | + | . | . | + | . | . | . | . | . | . | . | . |
| <i>Thelycrania sanguinea</i> (L.) Fourr.                    | +     | . | + | . | . | . | . | . | . | . | . | + | . | . |
| <i>Trollius europaeus</i> L.                                | .     | . | . | . | . | . | . | . | + | . | . | . | . | . |
| <i>Ulmus glabra</i> Huds.                                   | .     | . | + | . | . | . | . | . | + | . | . | . | . | . |
| <i>Urtica dioica</i> L.                                     | +     | + | . | . | . | . | . | . | + | + | . | + | + | + |
| <i>Vaccinum myrtillus</i> L.                                | .     | . | + | . | . | . | . | + | . | . | + | . | . | . |
| <i>Veronica chamaedrys</i> L.                               | .     | + | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>V. montana</i> L.                                        | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>Viburnum opulus</i> L.                                   | .     | . | . | . | . | . | . | . | . | . | . | + | . | + |
| <i>Vicia sylvatica</i> L.                                   | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>Vincetoxicum hirundinaria</i> Medicus                    | .     | . | . | + | . | . | . | . | . | . | . | . | . | . |
| <i>Viola palustris</i> L.                                   | .     | + | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Viola riviniana</i> Rchb.                                | +     | + | . | . | . | + | . | . | . | . | . | . | . | . |
| BRYOPHYTES                                                  |       |   |   |   |   |   |   |   |   |   |   |   |   |   |
| <i>Amphideum mougeotii</i> (B. & S.) Schimp.                | .     | . | . | + | . | . | . | . | . | . | . | . | . | . |
| <i>Anomodon attenuatus</i> (Hedw.) Huben                    | .     | . | . | . | . | . | . | . | + | . | . | . | . | . |
| <i>A. viticulosus</i> (Hedw.) Hook. & Taylor                | +     | . | . | + | . | . | . | . | . | . | . | . | . | . |
| <i>Atichum undulatum</i> (Hedw.) P. Beauv.                  | +     | . | . | . | + | . | . | . | . | . | . | . | . | . |
| <i>Brachythecium albicans</i> (Hedw.) B. & S.               | .     | . | . | . | . | . | . | . | . | . | + | . | . | . |
| <i>B. glareosum</i> (Bruch.) B. & S.                        | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>B. populeum</i> (Hedw.) B. & S.                          | +     | . | . | + | . | . | . | . | + | . | . | + | . | . |
| <i>B. rivulare</i> (Bruch.) B. & S.                         | .     | + | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>B. rutabulum</i> (Hedw.) B. & S.                         | +     | . | . | . | . | . | . | . | . | . | + | . | + | . |
| <i>Bryum pseudotriquetrum</i> (Hedw.) Schwaegr.             | .     | . | . | . | . | . | . | . | . | . | . | . | + | . |
| <i>Calypogeia fissa</i> (L.) Raddi                          | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>Camptothecium sericeum</i> (Hedw.) Kindb.                | .     | . | . | + | . | . | . | . | . | . | . | . | . | . |
| <i>Ceratodon purpurea</i> (Hedw.) Brid.                     | .     | . | . | . | . | . | . | + | . | . | . | . | . | . |
| <i>Cimacium dendroides</i> (Hedw.) Web. & Mohr.             | .     | . | . | . | . | . | . | . | . | + | . | . | . | . |
| <i>Cirriphyllum crassinervium</i> (Tayl.) Loeske & Flesich. | .     | . | + | . | + | . | . | . | . | . | . | . | . | . |
| <i>Conocephalum conicum</i> (L.) Dum.                       | +     | + | . | . | + | . | . | . | . | . | . | . | + | . |
| <i>Ctenidium molluscum</i> (Hedw.) Mitt.                    | .     | . | + | + | . | . | . | . | . | . | . | . | . | . |
| <i>Dicranella heteromalla</i> (Hedw.) Schp.                 | .     | . | . | . | . | . | + | . | . | . | + | + | . | . |
| <i>Dicranoweissia cirrata</i> (Hedw.) Lindb.                | .     | . | . | . | . | . | . | + | . | + | . | . | . | . |
| <i>Dicranum montanum</i> Hedw.                              | .     | . | . | . | . | . | . | + | . | . | . | . | . | . |
| <i>D. scoparium</i> Hedw.                                   | .     | . | . | . | . | . | . | . | + | . | . | . | . | . |
| <i>Encalypta ciliata</i> Hedw.                              | .     | . | . | . | . | . | . | . | + | . | . | . | . | . |
| <i>Eurhynchium confertum</i> (Dicks.) Milde                 | +     | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>E. schleideri</i> (Hedw. fil.) Lor.                      | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>E. striatum</i> (Hedw.) Schp.                            | .     | . | . | . | . | . | . | . | . | . | + | . | . | + |
| <i>Fissidens taxioli</i> (Hedw.) Juv.                       | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>Grimmia apocarpa</i> Hedw.                               | .     | . | . | . | . | . | . | . | + | . | . | . | . | . |
| <i>Hedwigia ciliata</i> (Hedw.) P. Beauv.                   | .     | . | . | + | . | . | . | . | . | . | . | . | . | . |
| <i>Hygroamblystegium irriguum</i> (Wils.) B. & S.           | .     | . | . | + | . | . | . | . | . | . | . | . | . | . |
| <i>Hylocomium splendens</i> (Hedw.) B. & S.                 | .     | . | . | . | . | . | . | . | . | . | + | . | . | . |
| <i>Hypnum cupressiforme</i> Hedw.                           | .     | + | . | . | . | + | . | . | . | + | . | . | . | . |
| <i>Lesuraea mutabilis</i> (Brid.) Lindb.                    | .     | . | . | . | . | . | . | + | . | . | . | . | . | . |
| <i>Metzgeria furcata</i> (L.) Dum.                          | .     | + | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Mnium undulatum</i> Hedw.                                | .     | . | . | . | . | . | . | . | . | . | . | . | + | + |
| <i>M. punctatum</i> Hedw.                                   | +     | . | . | . | . | . | . | . | . | . | . | + | . | + |
| <i>M. affine</i> Bland.                                     | .     | . | . | . | . | . | . | . | . | + | . | . | . | . |
| <i>Philonotus fontana</i> (Hedw.) Brid.                     | .     | . | . | . | . | . | . | . | . | . | . | . | + | . |
| <i>Plagiochila asplenoides</i> (L.) Dum.                    | .     | . | . | . | . | . | . | . | . | . | + | . | . | + |
| <i>Plagiothecium denticulatum</i> (Hedw.) B. & S.           | +     | . | . | + | . | . | . | . | . | . | . | . | + | + |
| <i>P. roseanum</i> (Hampe) Lindb.                           | .     | . | . | . | . | . | . | . | . | + | . | . | . | . |
| <i>P. sylvaticum</i> (Brid.) B. & S.                        | .     | + | . | . | + | . | . | . | . | + | . | + | + | + |
| <i>Polytrichum formosanum</i> Hedw.                         | .     | . | . | . | . | . | . | . | . | + | + | . | . | . |



|                                                   | SITES |   |   |   |   |   |   |   |   |   |   |   |   |   |
|---------------------------------------------------|-------|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BRYOPHYTES                                        | A     | B | C | D | E | F | G | H | I | J | K | L | M | N |
| <i>P. juniperinum</i> Hedw.                       | .     | . | . | . | . | . | . | + | . | . | . | . | . | . |
| <i>P. piliferum</i> Hedw.                         | .     | . | . | + | . | . | . | + | . | . | . | . | . | . |
| <i>Pseudoscleropodium purum</i> (Hedw.) Fleisch.  | .     | . | . | . | . | . | . | . | . | . | . | + | . | . |
| <i>Pylaisia polyantha</i> (Hedw.) B. & S.         | .     | . | . | . | . | . | + | . | . | . | . | . | . | . |
| <i>Rhytidiadelphus triquetrus</i> (Hedw.) Warnst. | .     | . | . | . | . | . | . | . | . | . | + | . | . | . |
| <i>Scapania nemorea</i> (L.) Dum.                 | .     | . | . | . | . | . | . | . | . | . | + | . | . | . |
| <i>Thuidium tamariscinum</i> (Hedw.) B. & S.      | .     | . | . | . | . | . | . | . | . | . | + | . | . | + |
| <i>Tortula ruralis</i> (Hedw.) Crome              | .     | . | . | . | . | . | . | . | + | . | . | . | . | . |
| <i>T. subulata</i> Hedw.                          | .     | . | . | . | . | . | . | . | + | . | . | . | . | . |
| <i>Trichostoma sinuosum</i> (Wils.) Lind.         | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>T. tenuirostre</i> (Hook. & Tayl.) Lind.       | .     | . | . | . | . | . | . | . | + | . | . | . | . | . |

*The Snail Fauna.* The presence or absence at the fourteen sites of 55 species of slugs and snails is presented in Table 2. The nomenclature follows Bishop (1976b). After elimination of molluscs of unique occurrence, 42 species remained. Following principal coordinates analysis, three axes could represent 44% of the total variance between sites. None of the three axes could be interpreted in terms of altitude, but axis 1 was correlated with pH ( $r_s = 0.48$ ,  $p = 0.04$ ). *Cochlicopa lubrica* and *Phenacolimax major* were found only in the less acidic woods, while *Drepanostoma nautiliforme*, *Limax dacampoi*, and *Oxychilus mortilleti* were remarkably tolerant of acidity.

The first axis scores for molluscs were correlated with the third axis scores for plants ( $r_p = 0.57$ ,  $p = 0.02$ ), not surprisingly, as both were correlated with pH. The second axis scores for molluscs were correlated with the second axis scores for plants ( $r_p = 0.60$ ,  $p = 0.01$ ). This direction of variation is hard to interpret, one end being represented at sites C, F, and G (with *Pteridium aquilinum*, *Anemone nemorosa*, *Discus rotundatus* and *Ena obscura*) and the other at sites E and I (with *Dryopteris pseudomas*, *Luzula nivea*, *Chilostoma zonata*, and *Arion silvaticus*). The scores for molluscs and bryophytes were uncorrelated.

Analysis of canonical correlations (Blackith and Reyment, 1971) between the site scores on the first three axes for vascular plants and molluscs gave: first canonical correlation 0.804, Wilk's lambda 0.261, chi-square 12.7, degrees of freedom 9,  $p = 0.17$  (not significant), indicating poor overall correspondence in the behaviour of plants and snails at the different sites.

DISCUSSION

The results of the analysis of the distribution of snails in acid woodland in the province of Novara closely parallel the results of the study in south-west Ireland. Flora and snail fauna have poor overall correspondence (Novara,  $p = 0.17$ ; Ireland,  $p = 0.10$ ), and pH is a poor measure for explaining overall variation in snail fauna. This is in contrast to the study in Somerset, where vegetation and pH were both highly effective in explaining distribution of snail fauna ( $p < 0.005$ ), the difference being due to the wider range of habitats sampled. In Ireland, where chemical analyses of soil and litter were available, litter minerals were shown to be most effective in explaining snail distribution. It was suggested that food protein made available by the organisms of litter decomposition might represent the major causal factor involved (Bishop, 1977a).

Future improvements in our understanding of the habitat distribution of terrestrial snails in acidic woodland are most likely to result from two lines of investigation: (1) Determination of



THE MOLLUSCA OF ACID WOODLAND

TABLE 2. Occurrence of Mollusca in fourteen sites in woodland in the Province of Novara, Italy

|                                            | SITES |   |   |   |   |   |   |   |   |   |   |   |   |   |
|--------------------------------------------|-------|---|---|---|---|---|---|---|---|---|---|---|---|---|
|                                            | A     | B | C | D | E | F | G | H | I | J | K | L | M | N |
| PROSOBRANCHIA                              |       |   |   |   |   |   |   |   |   |   |   |   |   |   |
| <i>Acicula lineata</i> (Draparnaud)        | +     | + | . | . | . | . | . | . | . | . | + | . | . | . |
| <i>Pieuracme bayoni</i> (Pollonera)        | .     | . | + | + | . | . | . | . | . | . | . | . | . | . |
| BASOMMATOPHORA                             |       |   |   |   |   |   |   |   |   |   |   |   |   |   |
| <i>Carychium minimum</i> Müller            | .     | . | . | . | . | . | . | . | . | . | + | . | . | . |
| <i>Carychium tridentatum</i> (Risso)       | +     | . | + | . | . | . | . | . | . | + | + | . | + | + |
| STYLOMMATOPHORA                            |       |   |   |   |   |   |   |   |   |   |   |   |   |   |
| <i>Acanthinula aculeata</i> (Müller)       | +     | . | + | . | . | . | . | . | + | + | . | . | + | + |
| <i>Aegopinella minor</i> (Stabile)         | .     | + | + | + | . | + | . | . | + | . | + | . | . | . |
| <i>Aegopinella pura</i> (Alder)            | .     | . | + | . | . | . | . | . | . | . | . | . | . | . |
| <i>Argna ferrarii</i> (Porro)              | +     | + | . | + | . | + | . | . | . | . | + | . | . | . |
| <i>Arion circumscriptus</i> Johnston       | .     | . | . | . | . | . | . | . | . | . | . | + | . | + |
| <i>Arion silvaticus</i> Lohmander          | .     | . | . | . | + | . | . | + | + | . | . | . | . | . |
| <i>Arion subfuscus</i> (Draparnaud)        | +     | . | + | . | + | . | . | + | . | + | + | + | . | . |
| <i>Ariunculus speziai</i> Lessona          | .     | . | . | . | . | . | . | . | + | . | + | . | . | . |
| <i>Balea perversa</i> (Linnaeus)           | .     | . | . | + | . | . | . | . | + | . | . | . | . | . |
| <i>Cepaea nemoralis</i> (Linnaeus)         | .     | + | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Charpentieria thomasiana</i> (Küster)   | +     | . | + | . | + | . | + | . | + | + | + | . | . | + |
| <i>Chilostoma zonatum</i> (Studer)         | +     | . | . | . | + | . | . | + | . | . | . | . | . | . |
| <i>Clausilia cruciata</i> Studer           | +     | + | + | . | + | . | . | . | + | + | . | . | . | . |
| <i>Clausilia dubia</i> Draparnaud          | .     | . | . | . | . | . | . | . | . | + | . | . | . | . |
| <i>Cochlicopa lubrica</i> (Müller)         | .     | . | . | + | . | . | . | + | . | . | . | . | . | . |
| <i>Cochlicopa lubricella</i> (Porro)       | .     | . | . | + | . | . | . | + | + | . | . | . | . | . |
| <i>Columella columella</i> (Martens)       | .     | . | . | . | . | . | . | + | . | . | . | . | . | . |
| <i>Columella edentula</i> (Draparnaud)     | .     | . | . | + | . | . | . | . | . | + | + | . | . | . |
| <i>Deroceras agreste</i> (Linnaeus)        | .     | . | . | . | . | . | . | + | . | . | . | . | . | . |
| <i>Deroceras laeve</i> (Müller)            | .     | . | . | . | + | . | . | . | . | . | + | . | . | + |
| <i>Deroceras pollonerai</i> (Simroth)      | +     | + | . | . | . | + | . | . | . | . | . | . | . | . |
| <i>Deroceras reticulatum</i> (Müller)      | .     | . | . | + | . | . | + | . | . | . | . | + | . | + |
| <i>Discus rotundatus</i> (Müller)          | +     | + | + | + | . | . | + | . | . | + | + | . | . | . |
| <i>Discus ruderatus</i> (Férussac)         | .     | . | . | . | . | . | . | + | . | . | . | . | . | . |
| <i>Drepanostoma nautiliforme</i> (Porro)   | +     | + | + | . | + | + | + | . | . | + | + | . | + | + |
| <i>Ena obscura</i> (Müller)                | +     | + | . | + | . | . | + | . | + | + | . | . | + | . |
| <i>Euconulus fulvus</i> (Müller)           | .     | . | . | . | . | . | . | + | + | . | + | . | . | . |
| <i>Euomphalia strigella</i> (Draparnaud)   | .     | . | . | + | . | + | . | . | . | + | . | . | . | . |
| <i>Helicodonta obvoluta</i> (Müller)       | +     | + | + | + | . | + | . | . | + | + | + | + | + | + |
| <i>Helix pomatia</i> Linnaeus              | .     | . | + | + | . | . | . | . | + | + | . | + | . | . |
| <i>Lauria sempronii</i> (Charpentier)      | .     | . | . | + | . | . | . | . | . | . | . | . | . | . |
| <i>Lehmania marginata</i> (Müller)         | +     | + | . | . | . | . | . | . | + | . | + | . | + | + |
| <i>Limax dacampoi</i> Menegazzi            | +     | + | + | . | + | + | + | . | . | . | + | . | . | . |
| <i>Limax maximus</i> Linnaeus              | .     | . | . | + | . | . | . | . | . | . | . | + | . | . |
| <i>Limax tenellus</i> Müller               | .     | . | . | . | . | . | . | + | . | . | . | . | . | . |
| <i>Macrogastra lineolata</i> (Held)        | +     | . | . | . | . | . | . | . | . | + | . | + | + | . |
| <i>Milax rusticus</i> (Millet)             | +     | + | + | . | + | . | . | . | + | . | + | + | + | . |
| <i>Monachoides incarnata</i> (Müller)      | +     | + | . | + | + | . | . | . | . | . | + | + | + | . |
| <i>Nesovitrea hammonis</i> (Ström)         | .     | . | . | . | . | . | . | + | + | . | . | . | . | . |
| <i>Nesovitrea petronella</i> (Charpentier) | .     | . | . | . | . | . | . | + | . | . | . | . | . | . |
| <i>Oxychilus glaber</i> (Rossmässler)      | .     | . | + | + | + | . | . | . | + | + | . | . | + | . |
| <i>Oxychilus mortilleti</i> (L. Pfeiffer)  | +     | + | + | . | . | . | + | . | . | . | + | + | . | . |
| <i>Phenacolimax major</i> (Férussac)       | .     | . | . | . | + | . | . | . | . | + | + | . | . | . |
| <i>Punctum pygmaeum</i> (Draparnaud)       | .     | + | . | + | . | . | . | + | + | + | . | . | . | . |
| <i>Retinella hiulca</i> (Albers)           | +     | + | . | . | + | . | . | . | . | . | . | . | . | + |
| <i>Succinea putris</i> (Linnaeus)          | .     | . | . | + | . | . | . | . | . | . | . | . | . | . |
| <i>Vallonia costata</i> (Müller)           | .     | . | . | + | . | . | . | . | . | . | . | . | . | . |
| <i>Vallonia excentrica</i> Sterki          | .     | . | . | + | . | . | . | . | . | + | . | . | . | . |
| <i>Vertigo pusilla</i> Müller              | .     | . | . | + | . | . | . | . | . | + | . | . | . | . |
| <i>Vertigo pygmaea</i> (Draparnaud)        | .     | . | . | + | . | . | . | . | . | . | . | . | . | . |
| <i>Vitrea subrimata</i> (Reinhardt)        | .     | . | . | + | + | . | . | . | + | . | . | . | . | + |



the dietary requirements of individual species. (2) Determination of the availability of suitable food in the natural environments. It is not safe to assume, as Boycott (1934) did, that food is always available in excess.

Failure to discover significant correlations between snail distribution and environmental factors could have further interpretations. Paul (1978) investigated the suggestion that the mollusc fauna of ancient woodland in Britain might resemble that known from fossils of the Atlantic optimum. He found, however, that many molluscs rapidly colonize new additions to old woods, only species classed as 'rare in East Anglia' being absent from isolated modern woods in the study area. Powell and South (1978) suggested that the distribution of mollusc species amongst 44 modern gravel-pit lakes could be largely determined by chance, rather than being attributable to any of the environmental factors which they measured. Capacity for dispersal must therefore be considered an important factor in determining distributions. The stability of an assemblage at a particular site should be assessed by repeated sampling over a number of years, prior to making firm assertions about the influence of the environment.

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# COEXISTENCE OF TWO CLOSELY RELATED SPECIES OF *ARION* IN NATURAL HABITATS

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*Abstract:* Detailed investigation of two areas on the Wirral Peninsula has revealed populations of *Arion ater* and *A. lusitanicus* in comparatively undisturbed habitats. These populations appear to be mutually exclusive. There are considerable differences in morph frequencies both between species and between populations of *A. lusitanicus*. *A. lusitanicus* appears frequently to mature early while still retaining some juvenile colour characters, and populations maintain a much higher density than do adjacent populations of *A. ater*. *A. subfuscus* is present but only with *A. lusitanicus*. Preliminary evidence is given that the colour morphs of *A. lusitanicus* are genetically determined. The significance of this type of distribution of closely related species is briefly discussed.

Early in a survey of variation in the *Arion ater* aggregate, it was noticed that in some areas of Thurstaston Common on the Wirral Peninsula (Fig. 1), individuals were of the typical black form and in other areas they were pale brown. It was decided to study this interesting phenomenon in detail.

On dissection the pale individuals were identified as *A. lusitanicus*. This species has been recorded in undisturbed habitats in the British Isles, in southern England, particularly Devon and Cornwall, in Wales and near the west coast of Ireland (Kerney, 1976). Ellis (1965) suggested that the species may be truly native to these areas. There are a number of records from garden habitats in central England and southern Scotland (Kerney, 1976) but they may be recent introductions. Little is known of its ecology (Quick, 1960) and no studies have been made on its microdistribution relative to *A. ater*.

The coexistence of two closely related species, so similar externally and both generalist feeders, is a very interesting ecological phenomenon. Much has been written on the relevance of Gause's Competitive Exclusion Principle to natural populations. Theories on the evolution of community structure and on patterns of species diversity are based on interpretations of the extent to which competition between closely related species occurs and of the outcome of such competition in the past (see Cody and Diamond, 1975). Many investigations have shown that, where closely related species are sympatric, direct competition is limited by basic differences in their niches, e.g. their physiological tolerances to climatic factors or food preferences (MacArthur, 1968). The populations at Thurstaston provide an opportunity for investigating the extent of interaction between these closely related *Arion* species in relatively undisturbed habitats.

The *A. lusitanicus* populations show considerable colour variation. An investigation of the mode of inheritance of this has begun and the variation within and between a number of populations is compared.



## STUDY AREA

The areas sampled intensively, Thurstaston Common and Caldy Hill (Fig. 1) are two of several sandstone hills rising above the Wirral clay plain. Both areas are maintained in relatively undisturbed condition by the National Trust and are used primarily for recreation. Sections of these areas are heavily wooded while others are covered by heather and gorse. Detailed maps of the areas are provided (Figs. 2 and 3). Garden and village collecting sites are shown in Fig. 1.



Fig. 1. Sampling sites.

## METHOD

*Samples.* Samples were collected at night in September, October and November, 1978. Sites were selected wherever one or more slugs were found. As the study progressed, areas of particular interest were searched intensively. No attempt was made to expend equal effort at all sites. Despite intensive searching, few *A. ater* were obtained at a number of sites and no slugs were found on the south-west slopes of Thurstaston Common.

Because *A. lusitanicus* was locally more abundant, the sampling sites for this species were generally smaller than for *A. ater*. Sites varied from about 9 m<sup>2</sup>, Caldy site 7, to about 100 m<sup>2</sup>, Thurstaston site 2.

*Scoring.* Two methods of scoring the colour of slugs were used. After examination of a number of samples, it was possible to ascribe individual *A. ater* to one of three colour classes and individual *A. lusitanicus* to one of four. In the second method, the Villalobos Colour Atlas, previously used by Cain and Williamson (1958) to describe colour variation in *A. ater* and *A. rufus*, was used to obtain quantitative colour records on the mantle, the foot fringe, and the foot both medially



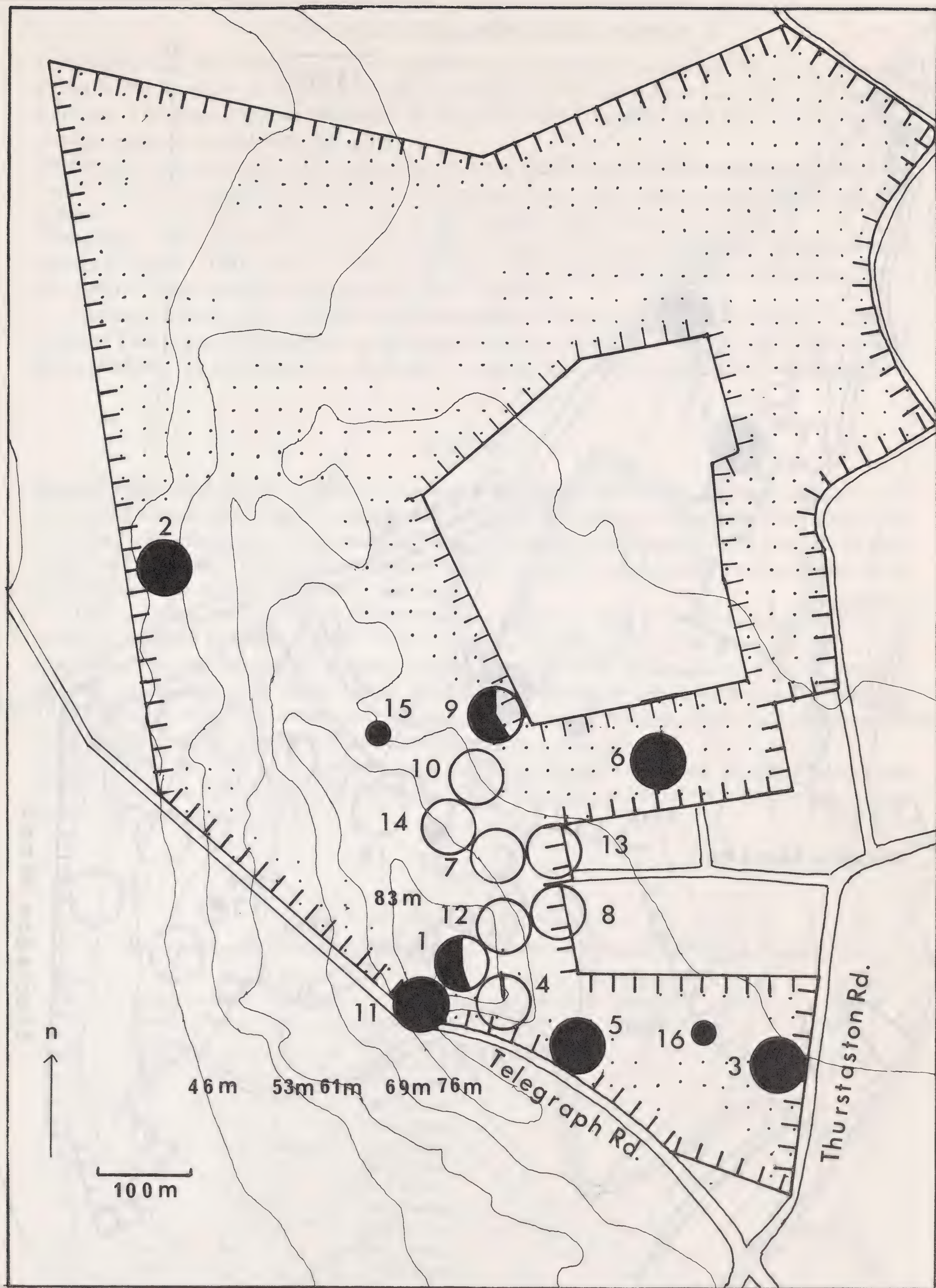


Fig. 2. Thurstaston Common sites showing the frequency of *A. ater* (black segments) and *A. lusitanicus* (white segments). The small circles refer to samples of 5 or less. Wooded sections of the Common have been stippled.



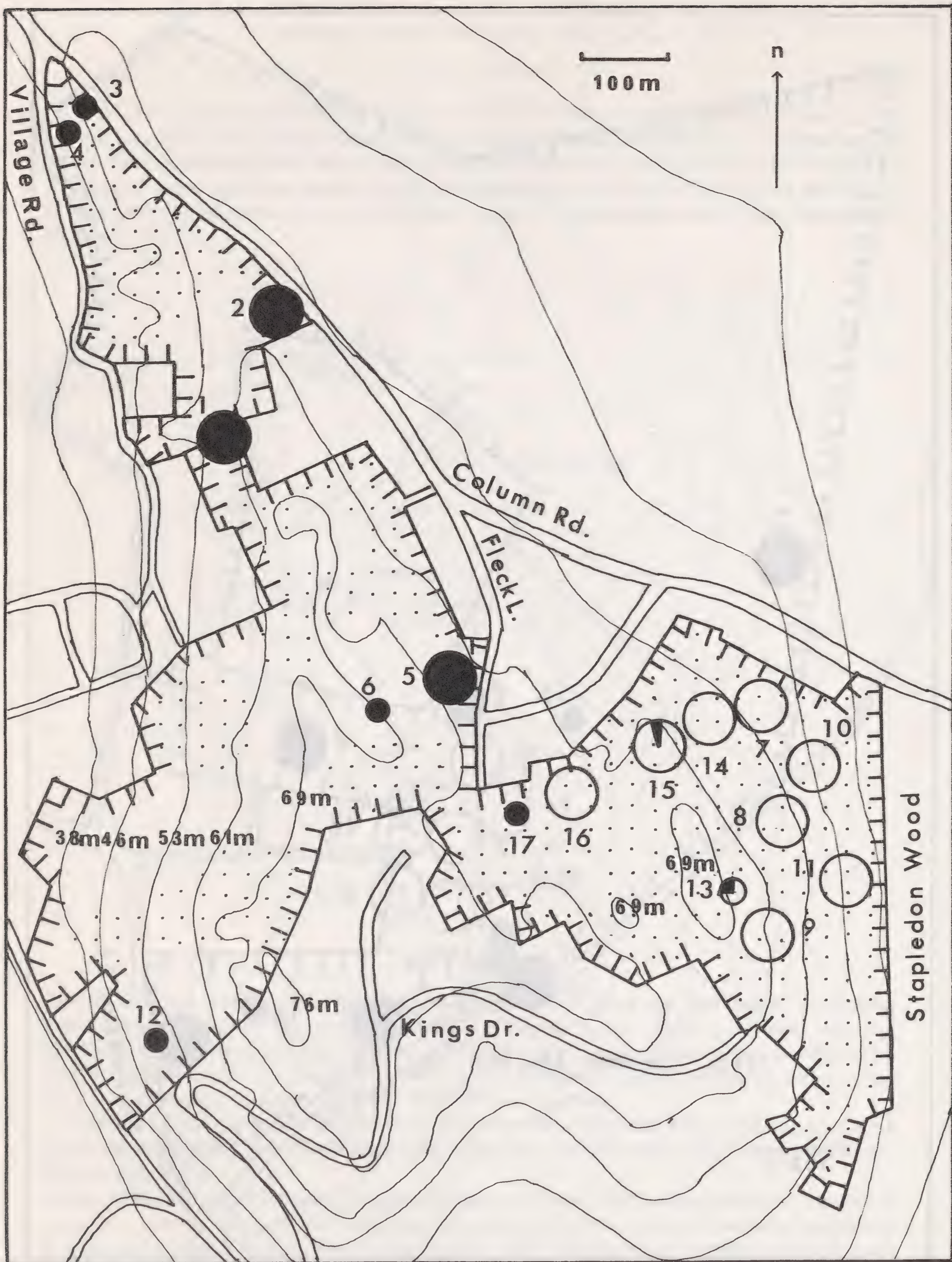


Fig. 3. Caldy Hill sites showing the frequency of *A. ater* (black segments) and *A. lusitanicus* (white segments). The small circles refer to samples of 5 or less. Wooded areas have been stippled.



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and marginally. The atlas provides a score between 1 and 38 for hue, 0 and 12 for saturation and 0 and 20 for intensity of each colour. All individuals were scored near a window with natural lighting. The colour classes obtained by the first method agreed with groupings of similar mantle scores obtained with the atlas.

*Breeding experiments.* Some of the slugs collected in the field were kept for breeding purposes. Pairs were maintained in plastic lunch boxes and fed on lettuce and finely ground rolled oats. The progeny were scored in the same way as field-caught individuals.

*Identification.* The reproductive tracts of specimens examined agreed with the descriptions and figures of Quick (1960) for *A. ater* and *A. lusitanicus*. The epiphallus and the terminal portion of the oviduct were strongly pigmented in all *A. lusitanicus*.

Almost all the *A. ater* exhibited the characteristic rocking motion while being handled for scoring. This behaviour could not be induced in any *A. lusitanicus*. This may be a simple test for distinguishing the two species in the field. It should, however, be verified by dissection.

## RESULTS

*Breeding experiments with A. lusitanicus.* It was not possible to score the progeny accurately until they were almost adult size. Considerable variation in colour and pattern was noticeable, however, when they were quite small (10 mm in length). Individuals which were to be light coloured (pale brown and dirty green brown) as adults lost the juvenile bands early and many individuals were clearly 'red' when small.

The variation among the adult progeny was similar to that of the field samples, *i.e.* they could be ascribed to one of the four colour classes (Table 1). The colour class of the parents is always represented among the progeny. This suggests that the variation in colour is controlled by one or two genes with major effects. This is similar to the situation in *A. ater* (Williamson, 1959). Because the slugs used as parents may have mated previously in the field, the mode of inheritance of these genes cannot be determined from these data.

*Spatial distribution.* The proportion of each species in samples from sites at Thurstaston and Caldy is shown in Figs. 2 and 3. The number in each sample and a brief comment on the habitat of the sites are given in Table 2.

TABLE 1

| Results of Breeding Experiments |             |               |        |        |             |            |                   |           |            |
|---------------------------------|-------------|---------------|--------|--------|-------------|------------|-------------------|-----------|------------|
| PARENTS                         |             |               |        |        |             | PROGENY    |                   |           |            |
| Cross No:                       | Origin      | Mantle scores |        |        | Class       | Pale brown | Dirty green brown | Red brown | Dark brown |
| 12                              | Crosby      | Hue 8         | Sat. 2 | Int. 9 | Green brown |            | 29                |           |            |
| 13                              | Crosby      | 7             | 2      | 7      | Green brown |            | 5                 |           |            |
| 14                              | Crosby      | 8             | 2      | 3      | Green brown | 3          | 13                |           |            |
| 26                              | Caldy       | 7             | 6      | 12     | Pale brown  |            |                   | 2         |            |
|                                 |             | 7             | 6      | 10     | Pale brown  |            |                   |           |            |
| 27                              | Caldy       | 7             | 8      | 1      | Dark brown  |            | 3                 |           | 2          |
|                                 |             | 7+            | 3      | 11     | Dark brown  |            |                   |           |            |
| 28                              | Caldy       | 6             | 7      | 7      | Red brown   |            |                   | 5         |            |
|                                 |             | 6             | 3      | 2      | Red brown   |            |                   |           |            |
| 32                              | Caldy       | 7             | 3      | 6      | Dark brown  |            |                   | 4         | 11         |
|                                 |             | 7+            | 2      | 3      | Dark brown  |            |                   |           |            |
| 33                              | Caldy       | 6-            | 7      | 4      | Red brown   |            |                   | 4         |            |
| 35                              | Caldy       | 8-            | 2      | 6      | Green brown |            | 2                 | 2         | 12         |
| 41                              | Thurstaston | 7             | 3      | 10     | Pale brown  | 7          | 11                |           |            |
| 45                              | Caldy       | 6             | 1      | 3      | Dark brown  |            |                   | 4         | 4          |
|                                 |             | 6             | 2      | 4      | Dark brown  |            |                   |           |            |



TABLE 2

Samples of large *Arion* at Thurstaston and Caldy

|             |    | Vegetation        | Aspect    | Number of      |                       | Presence of         |
|-------------|----|-------------------|-----------|----------------|-----------------------|---------------------|
|             |    |                   |           | <i>A. ater</i> | <i>A. lusitanicus</i> | <i>A. subfuscus</i> |
| Thurstaston |    |                   |           |                |                       |                     |
| Site        | 1  | Gorse thickets    | SE        | 16             | 13                    | no                  |
|             | 2  | Heather           | W         | 30             |                       | no                  |
|             | 3  | Wood              | SE        | 12             |                       | no                  |
|             | 4  | Gorse and grass   | SE        | 1              | 44                    | yes                 |
|             | 5  | Wood              | SE        | 12             |                       | no                  |
|             | 6  | Wood              | E         | 20             |                       | no                  |
|             | 7  | Heather           | E         |                | 41                    | yes                 |
|             | 8  | Heather and grass | E         |                | 25                    | yes                 |
|             | 9  | Birch wood        | E         | 22             | 16                    | yes                 |
|             | 10 | Heather           | SE        |                | 23                    | no                  |
|             | 11 | Gorse             | S         | 14             |                       | no                  |
|             | 12 | Heather           | SE        |                | 27                    | no                  |
|             | 13 | Wood              | SE        |                | 13                    | no                  |
|             | 14 | Heather           | E         |                | 19                    | yes                 |
|             | 15 | Heather           | NE        | 1              |                       | no                  |
|             | 16 | Heather           | SE        | 1              |                       | no                  |
| Caldy       |    |                   |           |                |                       |                     |
| Site        | 1  | Gorse             | NW        | 8              |                       | no                  |
|             | 2  | Wood              | N         | 8              |                       | no                  |
|             | 3  | Gorse             | N         | 5              |                       | no                  |
|             | 4  | Grass             | E         | 1              |                       | no                  |
|             | 5  | Heather           | Top       | 6              |                       | no                  |
|             | 6  | Heather           | SE        | 3              |                       | no                  |
|             | 7  | Wood              | SE        |                | 35                    | yes                 |
|             | 8  | Wood              | SE        |                | 18                    | yes                 |
|             | 9  | Gorse and wood    | SE        |                | 55                    | yes                 |
|             | 10 | Wood              | SE        |                | 36                    | no                  |
|             | 11 | Wood              | SE        |                | 19                    | no                  |
|             | 12 | Heather           | SW        | 3              |                       | no                  |
|             | 13 | Heather           | SE at top | 1              | 3                     | yes                 |
|             | 14 | Wood              | SE        |                | 41                    | no                  |
|             | 15 | Wood              | SE        | 1              | 15                    | no                  |
|             | 16 | Wood              | SE        |                | 14                    | no                  |
|             | 17 | Wood              | Top       | 1              |                       | no                  |

At the majority of sites only one of the two species *A. ater* and *A. lusitanicus* was found. The two species were found together in reasonable numbers at Thurstaston sites 1 and 9 (Fig. 2). Site 1 is adjacent to sites 5 and 11 where only *A. ater* was found and to site 4 where 44 *A. lusitanicus* and 1 *A. ater* were found. Site 9 was in a group of birch trees at the base of the heather-covered slope on the eastern side. Only *A. lusitanicus* was found on this slope and a large sample (site 10) was collected on the edge of the heather. Two sub-samples were collected at site 9; (A) at the southern end of the trees near the heather and (B) 15 m further into the trees. The proportion of *A. ater* was significantly greater at (B) (16 out of 18) than at (A) (6 out of 20). At both sub-sites, individuals of the two species were found within 0.5 m of each other. It is probable that at sites 1 and 9, sampling was along a boundary between the distributions of the two species. As the distributions of the two species appear to be mutually exclusive, it seems that there is little direct competition but further information on the area occupied by the populations and the distance moved by individuals each night in foraging is needed to evaluate the situation at the boundaries.



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TABLE 3

Typical Villalobos Atlas scores

| Species               | Colour class     | Mantle |      |      | Foot fringe |      |      | Marginal foot |      |      | Median foot |      |      |
|-----------------------|------------------|--------|------|------|-------------|------|------|---------------|------|------|-------------|------|------|
|                       |                  | Hue    | Sat. | Int. | Hue         | Sat. | Int. | Hue           | Sat. | Int. | Hue         | Sat. | Int. |
| <i>A. ater</i>        | Black            | —      | 0    | 1    | 7           | 5    | 9    | 8             | 1    | 8    | 8           | 2    | 12   |
|                       | Black            | —      | 0    | 1    | 7           | 2    | 5    | 7             | 3    | 13   | 7           | 3    | 13   |
|                       | Grey             | 7      | 1    | 6    | 8           | 3    | 11   | 8             | 2    | 13   | 8           | 3    | 14   |
|                       | Grey             | 7      | 1    | 7    | 7           | 10   | 13   | 8             | 7    | 15   | 8           | 7    | 15   |
|                       | Brown            | 7      | 2    | 3    | 6           | 6    | 9    | 7             | 6    | 7    | 7           | 10   | 10   |
|                       | Brown            | 6      | 3    | 2    | 6           | 8    | 10   | 7             | 2    | 8    | 6           | 2    | 6    |
| <i>A. lusitanicus</i> | Pale             | 7      | 7    | 11   | 7           | 7    | 15   | 8             | 6    | 15   | 8           | 6    | 15   |
|                       | Pale             | 7      | 5    | 8    | 7           | 8    | 15   | 8             | 6    | 16   | 7           | 8    | 18   |
|                       | Pale             | 7      | 9    | 13   | 7           | 10   | 17   | 8             | 6    | 15   | 8           | 6    | 15   |
|                       | Dirty green grey | 8      | 3    | 10   | 8           | 8    | 15   | 8             | 4    | 14   | 8           | 4    | 14   |
|                       | Dirty green grey | 8      | 2    | 6    | 8           | 8    | 16   | 8             | 3    | 13   | 8           | 3    | 13   |
|                       | Dirty green grey | 7      | 2    | 7    | 7           | 9    | 16   | 8             | 6    | 15   | 8           | 6    | 15   |
|                       | Dirty green grey | 8      | 2    | 8    | 7           | 7    | 13   | 8             | 4    | 14   | 8           | 4    | 14   |
|                       | Red brown        | 6      | 6    | 6    | 6           | 6    | 9    | 8             | 4    | 14   | 8           | 4    | 14   |
|                       | Red brown        | 6      | 5    | 9    | 6           | 6    | 10   | 8             | 4    | 13   | 8           | 4    | 13   |
|                       | Dark brown       | 6      | 2    | 2    | 6           | 2    | 3    | 8             | 4    | 14   | 8           | 4    | 14   |
|                       | Dark brown       | 7      | 2    | 3    | 7           | 2    | 6    | 8             | 3    | 13   | 8           | 3    | 13   |
|                       | Dark brown       | 8      | 1    | 1    | 8           | 4    | 1    | 8             | 3    | 12   | 8           | 3    | 12   |

Of the two species, *A. lusitanicus* has the more restricted distribution in this region. *A. ater* was found, at least in low numbers, on all slopes of both Caldy Hill and Thurstaston in a variety of habitats. *A. lusitanicus* occurs in woodland at Caldy and primarily in open grass and heather at Thurstaston, but just ranging into woodland. On both hills, *A. lusitanicus* was found only on the fairly steep eastern and south-eastern slopes. It was not found in the level woodland at the base of the eastern and southern slopes of Thurstaston (sites 3, 5, 6 and 11, Fig. 2).

A third related species, *A. subfuscus*, is common at both Thurstaston Common and Caldy Hill. Comprehensive samples of this species were not collected but its presence was recorded at a number of sites (Table 2). It was found only at sites where *A. lusitanicus* was collected.

*Population density.* The samples of *A. ater* are significantly smaller (mean  $13.9 \pm 2.3$ ) than those of *A. lusitanicus* (mean  $26.7 \pm 3.1$ ), although the areas searched and the time spent in searching for *A. ater* were considerably greater than for *A. lusitanicus*. The 64 *A. lusitanicus* from Caldy site 10 were collected from about 9 m<sup>2</sup> in less than 30 minutes and the 35 from Thurstaston site 4 from about 20 m<sup>2</sup> in a similar period. Less than 10 *A. ater* were collected from any site on any one night including those on which large samples of *A. lusitanicus* were obtained. Although no quantitative comparison is possible, it is evident that local populations of *A. lusitanicus* were considerably denser than those of *A. ater*.

*Variation in A. ater.* Specimens collected on the Wirral were dark with a dark foot fringe (Table 4). The sole of the foot was very dark near the margin but often lighter towards the middle. Typical scores from the Villalobos Atlas are given in Table 3.

Samples from more disturbed sites in villages (Table 4 bottom section) had a larger proportion of individuals with brown melanin than those from Caldy Hill, Thurstaston Common and the caravan site near the Dee at Thurstaston where individuals with black melanin predominated. No other conclusions regarding the frequencies of morph type and habitat can be made from these data.

*Variation in A. lusitanicus.* Four colour classes of *A. lusitanicus* were recognized; a pale brown, a dirty green brown, a red brown and a dark brown. Typical scores from the Villalobos Atlas for



TABLE 4

Number of *A. ater* in various colour classes

| Site                     | Black | Grey | Brown |
|--------------------------|-------|------|-------|
| Thurstaston 1            | 14    | 2    | 1     |
| 2                        | 30    |      |       |
| 3                        | 10    | 1    | 1     |
| 4                        | 1     |      |       |
| 5                        | 14    |      |       |
| 6                        | 19    | 1    |       |
| 9                        | 22    |      |       |
| 11                       | 3     |      | 1     |
| 15                       | 1     |      |       |
| 16                       | 1     |      |       |
| Caldy Hill 1             | 4     |      | 4     |
| 2                        | 4     |      | 1     |
| 3                        | 10    |      |       |
| 4                        | 1     |      |       |
| 5                        | 5     |      | 1     |
| 6                        | 3     |      |       |
| 12                       | 3     |      |       |
| 13                       | 1     |      |       |
| 15                       | 1     |      |       |
| 17                       | 1     |      |       |
| Thurstaston Caravan site | 13    |      |       |
| Disturbed sites:         |       |      |       |
| Burton (village)         | 12    |      | 8     |
| Burton (garden)          | 4     | 8    | 16    |
| Caldy (village)          | 1     |      | 7     |

these types are given in Table 3. Very few individuals did not fit clearly into one of these classes. The number in the various classes is given in Table 5. The overall pattern would not be altered by mis-scoring the few doubtful individuals. The foot fringe of all specimens was similar in hue to the mantle and body but was generally lighter. The sole of the foot was always pale.

A heterogeneity test within the Thurstaston samples was not significant at the 0.05 level. Because of the low numbers, only the four largest Caldys Hill sites could be tested, and in these the pale brown and green brown classes were pooled. This heterogeneity test was also not significant at the 0.05 level. Although there is little variation within each of the two areas, the variation between areas is significant. Pale brown and green brown predominate at Thurstaston, red brown and dark brown at Caldys.

Two samples of *A. lusitanicus* from gardens near Liverpool were available; both contained a very high proportion of dirty green brown individuals (Table 5, bottom section).

*Size of individuals.* It is impossible to obtain accurate measurements on slugs because of their ability to change shape. However, the length and breadth of contracted individuals allows some comparisons. The majority of *A. ater* were fully grown adults about 50 × 35 mm. The size range in *A. lusitanicus* was considerable; the largest was 55 × 38 mm while the majority was about 24 × 18 mm. Individuals of this smaller size were found mating in the field and produced fertile eggs in the laboratory. The ovotestes of some of the smaller individuals were still small. Many of the smaller individuals, particularly the darker ones, had the characteristic stripes of juvenile *A. lusitanicus*, but none of the larger ones was striped.



TWO CLOSELY RELATED SPECIES OF *ARION*

TABLE 5

Number of *A. lusitanicus* in various colour classes  
(Numbers in parentheses are those which were found difficult to score)

| Site           | Pale brown | Dirty green brown | Red brown | Dark brown |
|----------------|------------|-------------------|-----------|------------|
| Thurstaston 1  | 6 (1)      | 7                 |           |            |
| 4              | 16         | 28                |           |            |
| 7              | 21         | 20 (1)            |           |            |
| 8              | 13         | 12 (1)            |           |            |
| 9              | 11         | 5                 | (1)       |            |
| 10             | 13 (1)     | 10                |           |            |
| 12             | 19 (1)     | 8                 |           |            |
| 13             | 5 (1)      | 8                 |           |            |
| 14             | 9          | 10                |           |            |
| Caldy Hill 7*  | 2          | 3                 | 8         | 22         |
| 8              |            |                   | 5         | 13         |
| 9*             | 7          | 6                 | 11        | 31         |
| 10*            | 5 (1)      | 5 (1)             | 11        | 15         |
| 11             |            | 2                 | 10        | 7          |
| 14*            |            | 5                 | 11        | 25 (1)     |
| 15             | 1          |                   | 4         | 10         |
| 16             |            |                   | 2 (1)     | 14         |
| Garden samples |            |                   |           |            |
| Burton         | 1          | 19                |           |            |
| Crosby         | 1          | 16                |           | 1          |

\* Caldy Hill sites used in heterogeneity test.

## DISCUSSION

*A. lusitanicus* has a more restricted general distribution than *A. ater*. It is recorded from Portugal, France, Switzerland, the west coasts of Ireland and Wales, and southern England. *A. ater* occurs over most of Europe, in Russia and Iceland (Quick, 1960). Quick has suggested that the actual distribution of *A. lusitanicus* may be greater than this. Because of their external similarity and the considerable colour variation in each species, individuals of *A. ater*, *A. rufus* and *A. lusitanicus* can only be accurately identified after examination of the reproductive tracts. Although this is a simple procedure, there are few records of *A. lusitanicus* from habitats other than gardens in Britain (Kerney, 1976).

Cain and Currey (1963) reported that there were often sharp boundaries between the micro-distributions of the closely related species *Cepaea nemoralis* and *C. hortensis* on the Marlborough Downs. The pattern of micro-distributions was consistent with the hypothesis that similar climatic factors such as temperature, were determining both the broad ranges of the species and their local distributions. The situation in *Cepaea* has been reviewed by Jones, Leith and Rawlings (1977). Cameron (1969, 1970) found similar patterns of micro-distributions of *C. nemoralis*, *C. hortensis* and *Arianta arbustorum* at Rickmansworth and in Derbyshire. In laboratory studies, Cameron (1970) showed that temperature could be important in determining the local distributions of these species. Mordan (1977) demonstrated that interspecific differences in local distribution and abundance of *Aegopinella nitidula* and *A. pura* can be related to climatic factors.

The fact that there is little overlap in the micro-distributions of *A. ater* and *A. lusitanicus* at Caldys and Thurstaston, and that *A. subfuscus* was found only in association with *A. lusitanicus* suggests that as far as these species are concerned, there is a major environmental difference between the areas occupied by *A. lusitanicus* and *A. ater*. This environmental difference is more



likely to be associated with aspect than vegetation as can be seen in Table 2. Although *A. lusitanicus* may have a broader distribution than that recorded, it is a more southerly species than *A. ater* (Quick, 1960). Gregory (1953) in discussing the climate of Merseyside, states that considerable climatic differences can occur over short distances in the region due to topographical features. The sandstone hills of the Wirral have a milder climate than the surrounding plain principally because of the gravity flow of cold air down the slopes. The south-eastern and eastern slopes of these hills are also protected from the majority of strong winds which comes from the west. No measurements were made of the micro-climate during this survey, but it is not unreasonable to suggest that the eastern and south-eastern slopes of Caldy and Thurstaston occupied by *A. lusitanicus* have a milder micro-climate than other parts of the hills, and that the climatic factors important in determining the broad ranges of *A. lusitanicus* and *A. ater* are also important in determining the local distributions of populations.

Even where the pattern of local distributions of closely related species can be correlated with their physiological tolerance to climatic factors, questions concerning the importance of competition between the species remain unanswered. The pattern of distributions may be caused by competition, the outcome of which is determined in part by the different responses of the species to the particular micro-climate at any place. A study of the movement of individuals and the area occupied by the populations will provide information on the extent of interaction between individuals at the boundaries of the distributions.

One interesting feature of the present study is that local populations of *A. lusitanicus* are considerably larger than those of *A. ater*, the more widely distributed species. This may be related to the next point discussed.

A feature of the data is the relatively high proportion of *A. lusitanicus* which had juvenile characteristics, namely small size and banding. These individuals were mating in the field and many produced fertile eggs. It would be interesting to compare the development in these populations with that in populations near the centre of its range. Since *A. lusitanicus* mate when small, care should be taken to isolate individuals early in any breeding programme.

At present, there is no information on the cause of differences in frequency of colour forms of *A. lusitanicus* at Thurstaston and Caldy. It may be related to differences in habitat; woodland at Caldy and open heather and grass at Thurstaston. If it is, then the pattern in variation is opposite to that accepted in *A. ater* where woodland populations are generally lighter than those from open habitats (Williamson, 1959).

#### ACKNOWLEDGEMENTS

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## ADDENDUM

### NOTE ON THE FORM OF *Arion lusitanicus* MABILLE ON THE WIRRAL PENINSULA

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I am indebted to Miss Stella Davies for information on the two forms, at present included under *Arion lusitanicus* Mabilie, which occur in Britain, and for living material of one of them. One is described by Quick (1952, 1960) and also by Ellis (1964, excluding the figured specimen from Alphington, Devon). The other is described by Ellis (1965). In the Appendix to the reprint of his book (1969) Ellis was compelled by lack of space merely to mention the existence of two forms, without giving details. Miss Davies writes 'Every population I have seen . . . belongs to one form or the other—never mixed.' It seems probable, therefore, that the two forms are good species.

Dissection of specimens collected by Mr. Roger Middleton this year (1979) from the area investigated by Brian Conroy on Thurstaston Common (Wirral) in 1978 confirms that they are the form figured by Quick from Durham. A specimen given me by Mrs. N. F. McMillan from her garden at Bromborough (Wirral) is also of this form. Live specimens from Dr. C. R. C. Paul taken at Burton (Wirral) agree in externals.

One of Miss Davies's specimens was also dissected and shows marked differences in the genitalia. Quick (1952, fig. 5, copied in 1960, fig. 5E) gives a picture of the ligula of the Durham form; Ellis does not figure it for his form from South Devon. The ligula in Thurstaston specimens is a massive structure, in the form of a double U. The ends of the limbs are near the entry of the thinwalled portion of the free oviduct into the thick-walled one, the bends are not far from the entry of the latter into the atrium. One U is nested inside the other, and both are thick opaque fleshy folds, of fairly uniform height, much frilled all along their free edges. The limbs of each U are about equal in length, thickness and frilling. Quick's figure gives the general appearance if one merely slits open the muscular portion and peeps inside—it shows the outer aspect of both limbs of the outer U, but nothing of the inner U, nor that the limbs shown are joined as a U at the atrial end.

The ligula in Miss Davies's specimen is also U-shaped, but single and very little frilled, with both limbs and bend much thinner. It is higher at the bend, which forms a sort of lax pocket. One limb is shorter and less developed than the other, and both, in this specimen which was fully mature—indeed, eggbound—when it died, much more translucent than in the Thurstaston specimens, in which the ligula is solid-looking and more or less opaque even in the



freshly-dead animal. The thickwalled part of the free oviduct is also stouter in Thurstaston material, and if the animal is dissected from the ventral surface, it stands out almost like a dart-sac of a helcid, apparently blind. The thin-walled part lies beneath it, and retraces its course somewhat to enter the thick-walled part just behind its apparently blind apex. In Miss Davies's specimen, the thin-walled part merges into the thick-walled at much less of an angle and it is easy to see at a glance that both are parts of a continuous tube.

In the specimens I have seen from Thurstaston, there is a good scatter of pigment on the lower part of the penis, near where it enters the atrium. The pigment on the oviduct is much less in comparison, neither as thick nor arranged in so definite a pattern as is shown by Quick (1952 fig. 1; copied, 1960, as fig. 5A). In some specimens it seems to be absent from the oviduct, and is often not clearly visible there in preserved material. Miss Davies informs me that pigment may or may not occur in either form, and cannot be used as a distinguishing character.

I am indebted to Mrs. N. F. McMillan, Mr. Roger Middleton and Dr. C. R. C. Paul for material from the Wirral, and especially to Miss S. M. Davies for material of the other form and much useful information. Further work on this subject is being done by Miss Davies. A voucher specimen from Thurstaston with the ligula exposed is deposited in the collections of the British Museum (Natural History), registration number 1979224.

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# OBSERVATIONS ON THE DISPERSAL OF TWO SPECIES OF BRITISH LAND SNAIL

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(Read before the Society, 19 January 1980)

*Abstract:* The overnight movements of *Candidula intersecta* (Poiret) and *Cernuella virgata* (Da Costa) were observed in the Cotswolds by releasing marked snails and measuring the distances moved in the subsequent 24 hours. *C. virgata* moved further than *C. intersecta*, the maximum distances moved being approximately 300 cm and 120 cm respectively. *C. virgata* showed different behaviour depending on the microhabitat in which it was released. The difficulties of interpretation of this kind of study are discussed, particularly those relating to unmonitored environmental factors, condition of the experimental animals and the experimental procedure adopted.

Paul (1978) noted the lack of information available concerning the actual or potential rate of movement of molluscs both into new environments and within existing habitats. He also noted that in mark-release experiments, handling and overcrowding of the animals at the release point might have a significant effect on the results obtained. Experiments were therefore carried out on the overnight movements of two species of helicelline snails, *Cernuella virgata* (Da Costa) and *Candidula intersecta* (Poiret), with a view not only to relating the results to the long-term dispersive potential of the two species, but also to investigating the effects of the experimental procedure on the results.

The experiments were done as part of undergraduate field course projects on Rodborough Common, 2 km south of Stroud, Gloucestershire (map reference SO 849030) during the autumns of 1977 and 1978. The nomenclature used is that of Waldén (1976).

## THE STUDY AREA

Rodborough Common is an open area sloping steeply down to the south and west. At the top the ground flattens out and is partly occupied by houses and gardens. The lower slopes of the common are inhabited exclusively by *C. intersecta*. The vegetation here consists of a very low cover (up to 10 cm but mostly well below that) of plants characteristic of open, dry and highly calcareous areas, for instance *Helianthemum chamaecistus* Mill. (common rock rose), *Filipendula vulgaris* Moench (dropwort) and *Carlina vulgaris* L. (carline thistle). These low plants are interspersed with taller stems of grasses, which at the time of the studies were mostly dead or senescent. Some small areas of bare ground are exposed between the vegetation.

At the top of the area investigated *C. virgata* predominates. A stone wall and some bushes act as a windbreak. The terrain is flat and carries lush, relatively uniform vegetation, consisting largely of grass up to 50 cm high interspersed with taller patches of *Cirsium arvense* (L.) Scop. (creeping thistle). *C. virgata* tended to cluster on these thistles which were dead or senescent at the time of the studies. No bare earth is exposed.



Thus the habitat occupied by *C. intersecta*, although more diverse in species of plants than that occupied by *C. virgata*, is also more uniform in that the constituent species are more homogeneously intermingled. This association between habitat type and distribution of these two species of snail agrees with that found in other parts of the Cotswolds by P. Tattersfield (personal communication).

### METHODS

Seven experiments were carried out and these have been summarized in Table 1. In each experiment sixty snails were marked with spots of enamel paint and released from marked positions, and the horizontal distances travelled by the snails during the subsequent 24 hours were recorded. Only adult or near-adult snails were used. They were all collected a few minutes before marking and releasing them, and from areas near the release points. These were within the areas commonly inhabited by that species on the common. *C. virgata* was collected mostly from the thistles it tended to cluster on. In 1977 both experiments with *C. intersecta* were carried out over the same 24 hour period and the experiments with *C. virgata* over the following 24 hour period. In 1978 all three experiments were carried out over the same 24 hour period.

In experiments 1 to 5 (Table 1) each snail was marked with a single spot of paint on the apex of the shell and placed within a 2 cm radius of a small cane stuck in the ground. Only small numbers of snails were already present near the release points. These were ignored. One experiment was performed for *C. intersecta* in 1977 (experiment 1) and one in 1978 (experiment 2), both within similar habitats. Since the habitat of *C. virgata* is less uniform in terms of the intermingling of the plants, a comparison was made between the movement of *C. virgata* released in areas with few (1977) and no (1978) thistles within 3 m of the release points (experiments 3 and 4 respectively), and of snails released actually within a clump of thistles about 1 m in diameter (experiment 5).

In order to investigate the effects of disturbance and overcrowding at the release point, experiments 6 and 7 (Table 1) were performed in which snails were marked with a unique combination of colours and replaced in their original positions. A cocktail stick marked with the same combination of colours was stuck in the ground beside each snail, marking its initial position. The results from these experiments were compared with those from the experiments in which all sixty snails were released from the same point.

TABLE 1

Summary of experiments.

| experiment | species              | year | habitat              | mode of release | fig. |
|------------|----------------------|------|----------------------|-----------------|------|
| 1          | <i>C. intersecta</i> | 1977 | lower slope          | single point    | 1a   |
| 2          | <i>C. intersecta</i> | 1978 | lower slope          | single point    | 1b   |
| 3          | <i>C. virgata</i>    | 1977 | grass (few thistles) | single point    | 2a   |
| 4          | <i>C. virgata</i>    | 1978 | grass (no thistles)  | single point    | 2b   |
| 5          | <i>C. virgata</i>    | 1978 | thistles             | single point    | 4    |
| 6          | <i>C. intersecta</i> | 1977 | lower slope          | where found     | 5a   |
| 7          | <i>C. virgata</i>    | 1977 | grass (few thistles) | where found     | 5b   |

Frequency diagrams showing distances moved from the release points, grouped into 20 cm classes, were drawn (figs. 1, 2, 4 and 5) and compared with each other by  $\chi^2$  tests. In some cases the 20 cm classes were lumped to give adequate expectancies. Estimates of the variance and kurtosis of these distributions were calculated using the following relations:



$$\text{variance of dispersal} = \frac{\sum r^2 f}{n-1}$$

$$\text{kurtosis of dispersal} = \frac{(n-1)n(n+1)\sum r^4 f}{(n-2)(n-3)(\sum r^2 f)^2} - \frac{3(n-1)^2}{(n-2)(n-3)}$$

in which  $r$  is the median value of each 20 cm class

$f$  is the number of observations in each class

$n$  is the total recaptures

These equations are modifications of those used by Dobzhansky and Wright (1943), the extra terms involving  $n$  being corrections for bias in small samples (personal communication, Dr. J. J. D. Greenwood).

If dispersal is random, the histograms should look like half normal distributions with the axis being the release point. A value of zero for kurtosis indicates no departure from random. If kurtosis is less than zero, the distribution is platykurtic; if greater, leptokurtic. Departure from random can be tested by the  $t$ -test with an infinite number of degrees of freedom:

$$t = \frac{\text{kurtosis}}{\text{standard error of kurtosis}}$$

where s.e. of kurtosis is the square root of:

$$\frac{24 n(n-1)^2}{(n-3)(n-2)(n+3)(n+5)}$$

The values obtained for variance and kurtosis are given in Table 2.

TABLE 2

Values of variance and kurtosis.

| fig. | variance<br>(m <sup>2</sup> ) | kurtosis | departure from zero    |
|------|-------------------------------|----------|------------------------|
| 1a   | 0.075                         | 1.346    | leptokurtic $p < 0.05$ |
| 1b   | 0.175                         | 0.554    | n.s.                   |
| 2a   | 1.601                         | -0.370   | n.s.                   |
| 2b   | 2.479                         | -1.034   | n.s.                   |
| 4    | 0.172                         | -0.191   | n.s.                   |
| 5a   | 0.052                         | 2.576    | leptokurtic $p < 0.01$ |
| 5b   | 1.423                         | -0.119   | n.s.                   |

## RESULTS

Over 70% recapture was achieved in all experiments except numbers 6 (47%) and 7 (55%) in which difficulty in finding some of the cocktail sticks decreased the number of measurements taken. The frequency diagrams for *C. intersecta* released from a single point in 1977 (experiment 1, fig. 1a) and in 1978 (experiment 2, fig. 1b) are significantly different (when values for distance moved are lumped into the groups 0–20 cm, 21–40 cm, and 41 cm and above,  $\chi^2$  with 2



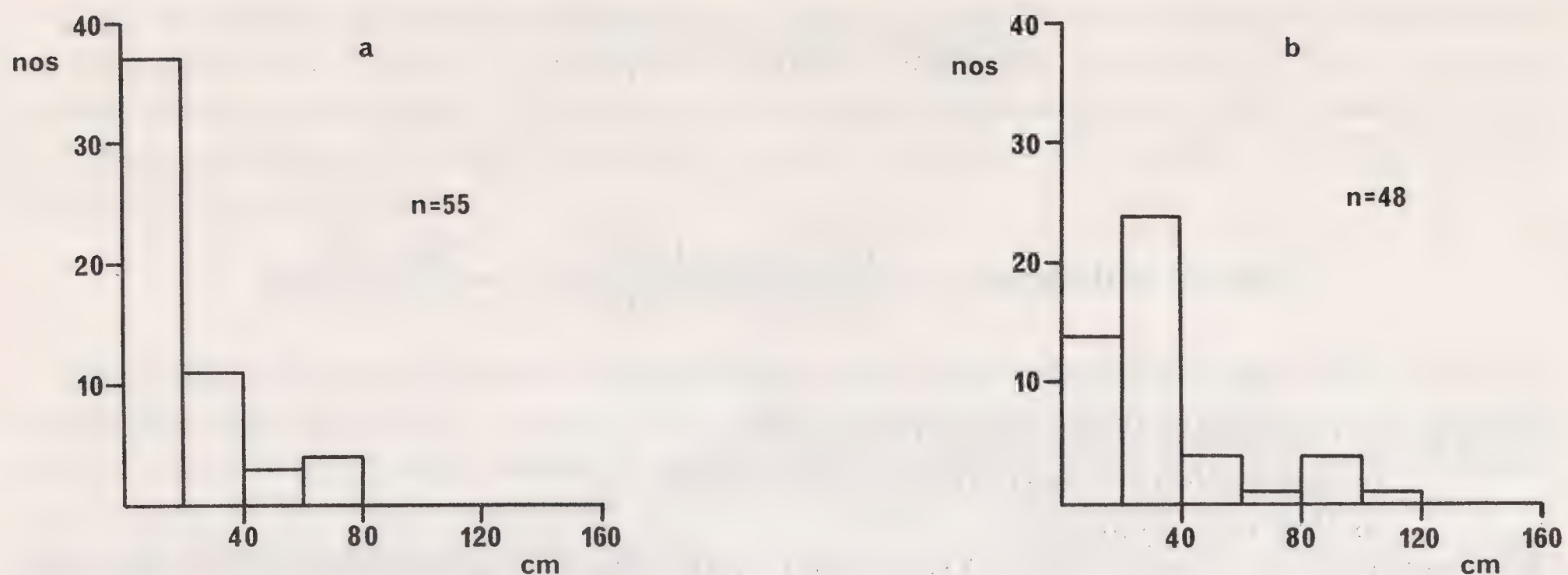


Fig. 1. Distances moved overnight by *C. intersecta* released from a single point. a - 1977; b - 1978. In this and all other figures, n = total recaptures.

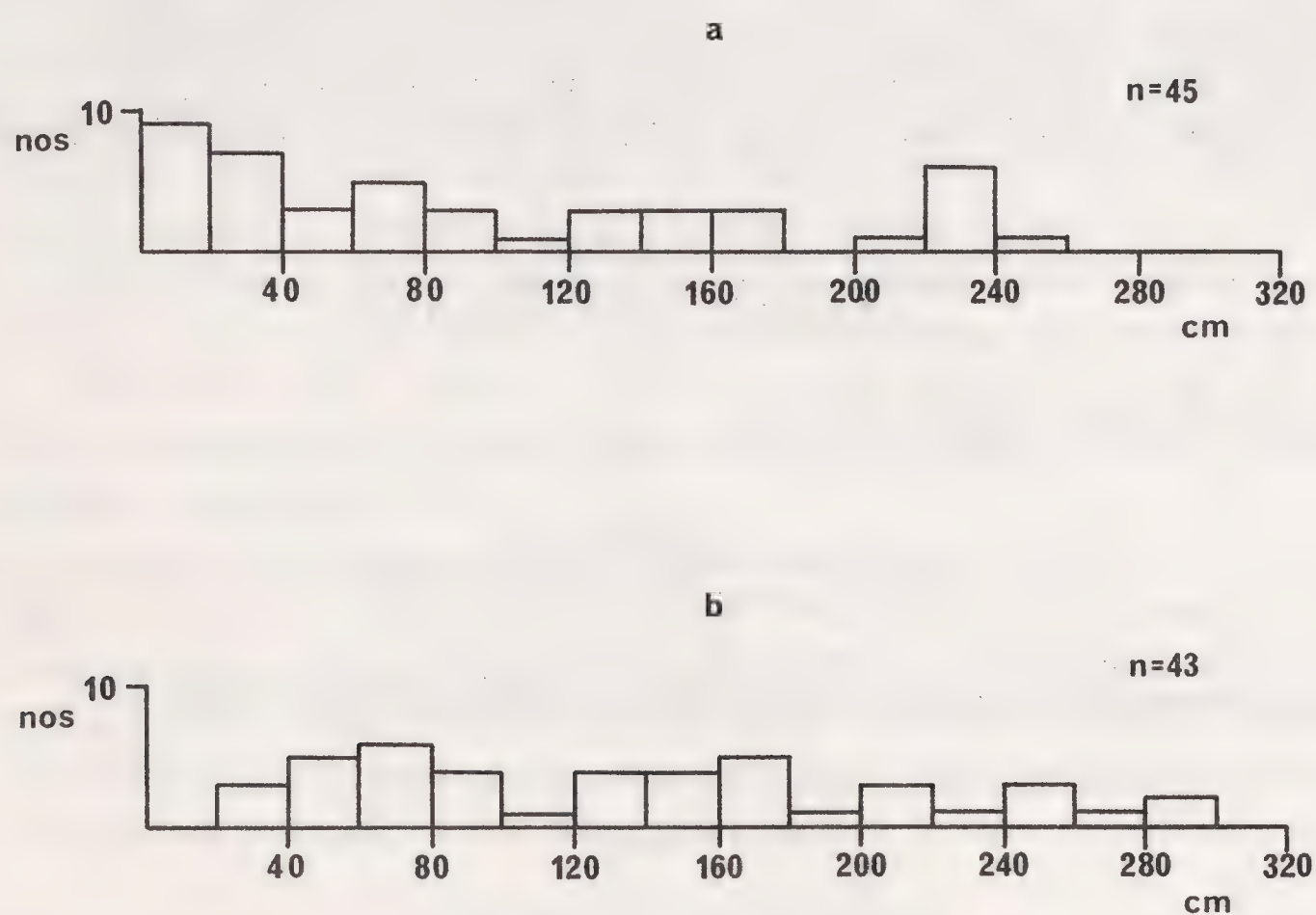


Fig. 2. Distances moved overnight by *C. virgata* released from a single point in an area with few (1977) or no (1978) thistles. a - 1977; b - 1978.

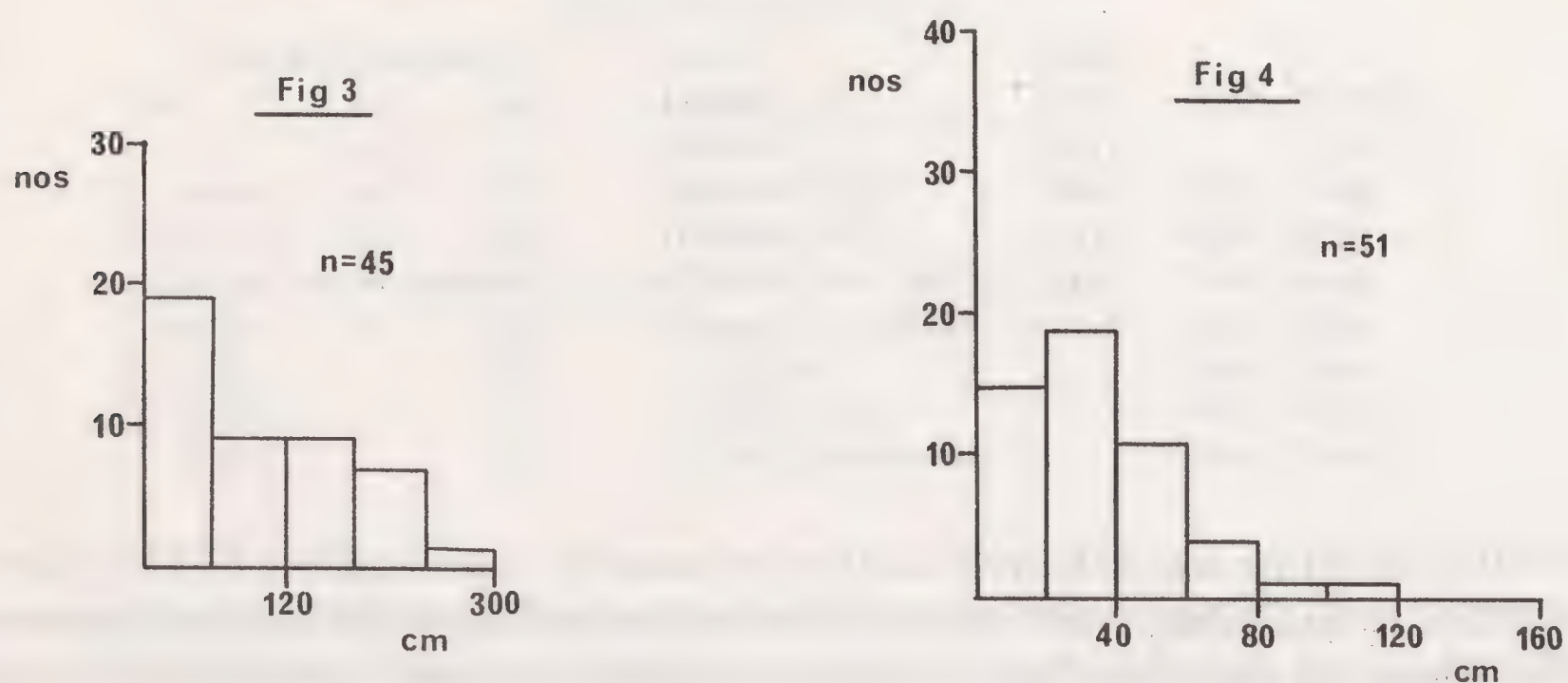


Fig. 3. Data in fig. 2a grouped in to 60 cm classes. Fig. 4. Distances moved overnight by *C. virgata* released from a single point in a clump of thistles.



d.f. = 15.3;  $p < 0.001$ ). The distribution in fig. 1a is significantly leptokurtic ( $p < 0.05$ ) but fig. 1b does not differ significantly from a random dispersal pattern. However, the overall picture is similar to that in fig. 1a inasmuch as most of the animals remained within 40 cm of the release point.

Three of the frequency diagrams for *C. virgata* (figs. 2a, 2b, 5b) show no significant departure from a random pattern of dispersal. These three diagrams appear at first sight to indicate platykurtosis, but if the observations are lumped into the groups 0–60 cm, 61–120 cm, 121–180 cm, 181–240 cm, and 241–300 cm, the random pattern is more apparent visually. This has been done for fig. 2a to give fig. 3. When *C. virgata* was released in an area with few thistles (experiment 3, fig. 2a) or no thistles (experiment 4, fig. 2b) there was no significant difference between the results (when values for distance moved are lumped into the groups 0–60 cm, 61–120 cm, 121–180 cm, and 181 cm and above,  $\chi^2$  with 3 d.f. = 5.8). There was, however, a highly significant difference in both 1977 and 1978 between these results for *C. virgata* and the results described above for *C. intersecta* in experiments 1 and 2 (when values are lumped into the groups 0–20 cm, 21–40 cm, and 41 cm and above,  $\chi^2$  with 2 d.f.  $> 30$  and  $p < 0.001$  in both cases).

However, in 1978 when released amongst a clump of dead thistles (experiment 5, fig. 4) *C. virgata* moved much less horizontally than when released in an area with no thistles (experiment 4, fig. 2b). This difference was significant (when values are lumped into the groups 0–20 cm, 21–40 cm, and 41 cm and above,  $\chi^2$  with 2 d.f. = 35.5;  $p < 0.001$ ).

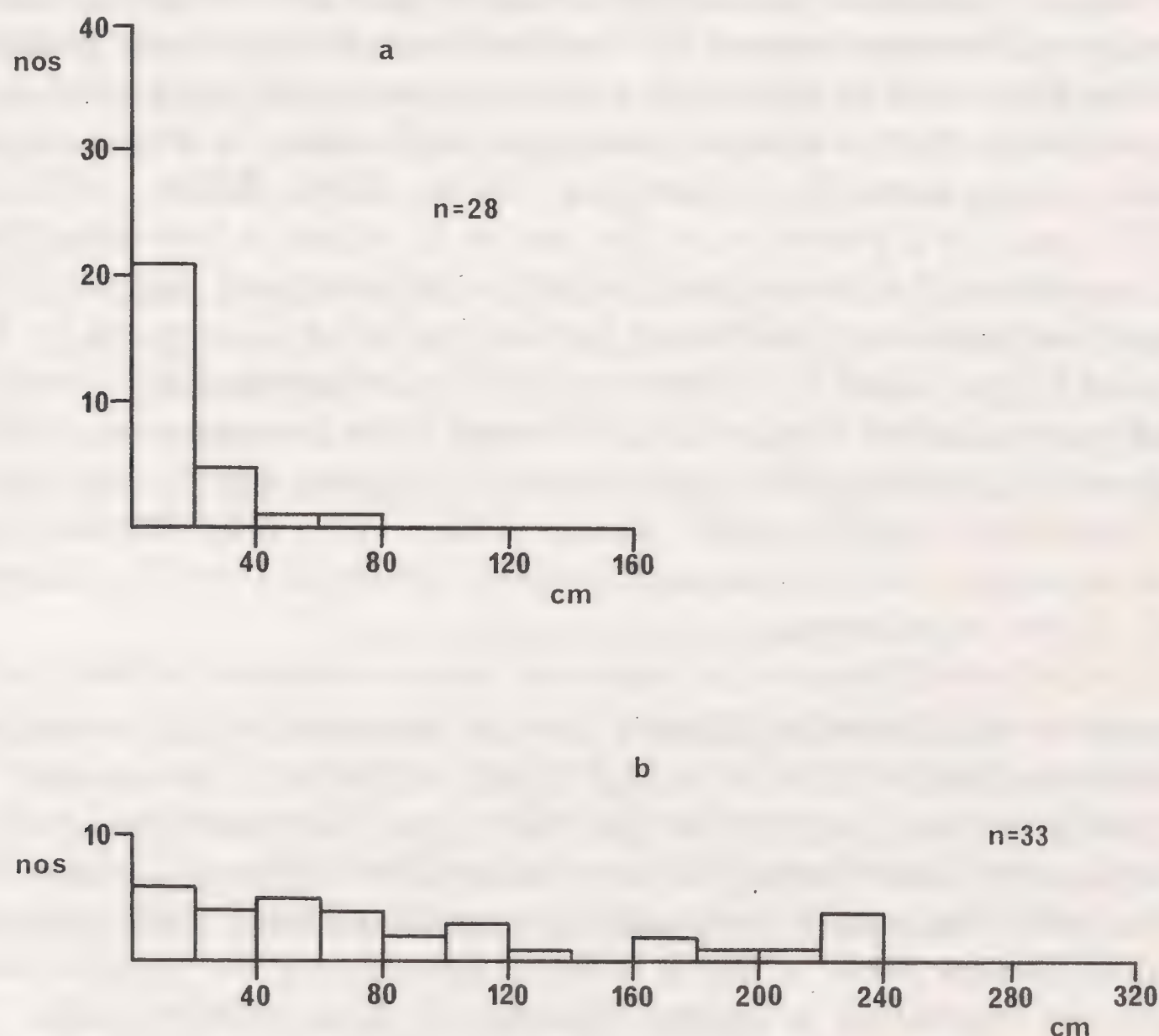


Fig. 5. Distances moved overnight by snails released where found. a – *C. intersecta*; b – *C. virgata*.

In 1977, when both *C. intersecta* and *C. virgata* (in an area with few thistles) were marked and released where found (experiments 6 and 7, figs. 5a and 5b), the distances moved were not significantly different from those when snails of each species were released from a single point (experiments 1 and 3). (For *C. intersecta* when values are lumped into the groups 0–20 cm, 21–40 cm, and 41 cm and above,  $\chi^2$  with 2 d.f. = 0.7. For *C. virgata* when values are lumped into the groups 0–40 cm, 41–80 cm, 81–120 cm, and 121 cm and above,  $\chi^2$  with 3 d.f. = 2.2). The



pattern of dispersal for *C. intersecta* was significantly leptokurtic ( $p < 0.01$ ). The difference between the two species which was apparent when snails were released from a single point was again found and was significant (when values are lumped into the groups 0–20 cm, 21–40 cm, and 41 cm and above,  $\chi^2$  with 2 d.f. = 25.9;  $p < 0.001$ ).

## DISCUSSION

Some work has been published on the movement of snails within habitats over a longer period of time than considered here and for a number of different species, notably: *Cepaea nemoralis* (L.) (Lamotte, 1951; Goodhart, 1962; Murray, 1962; Cain and Currey, 1968; Cameron and Williamson, 1977), *Theba pisana* (Müller) in South Africa (Hickson, 1972) and in Cornwall (Humphreys, 1976), and *Helix pomatia* L. (Pollard, 1975). All these studies were concerned with the observed movement within a habitat over the stated length of time and did not attempt to relate this to potential movement either within or between habitats as did Paul (1978). He was concerned with colonization by *Aegopinella nitidula* (Draparnaud) and *Trichia plebeia* (Draparnaud) and measured the movement of his snails on three consecutive days. Shachak, Orr and Steinberger (1975), concerned with seasonal differences in activity of *Sphincterochila* (S.) *zonata* (Bourguignat) (= *S. boissieri* Charpentier) in Israel, recorded overnight movements of their snails at different times of year and related this to the annual climatic cycle.

Before inferring anything about the dispersive potential of the two species used in the present study, the difficulties of interpretation of the results obtained in this study in particular, and in other studies of this kind must be discussed. Activity in most land snails is known to be related not only to seasonal differences but also to short-term differences in weather conditions, snails being least active when humidity is low (e.g. Wells, 1944; Bailey, 1975; Cameron and Williamson, 1977) and this is known to be the case for *C. virgata* in Australia (Pomeroy, 1969). Weather conditions during the present study could not be monitored, and some difference could explain the small but significant difference in the results for *C. intersecta* in 1977 and 1978 (experiments 1 and 2, figs. 1a and 1b). Pomeroy (1969) also showed that juvenile *C. virgata* were more active and moved further than adults. Although large animals were used in the present study, they may not all have been fully grown since it is known that *C. intersecta* in Devon does not breed until November and December (Baker, 1968). There may therefore have been some heterogeneity in behaviour both within and between species as a result of animals of different ages being used in the experiments.

It is not clear whether differences in behaviour between species in this type of experiment are true differences or result from the different habitats in which the snails are released. The fact that *C. virgata* showed different behaviour depending on whether it was released in a clump of thistles or in a thistle-free area suggests the possibility that *C. intersecta* might also move further (or less far) than this study has shown, if it were released in a different habitat. It must also be remembered that only the overall horizontal distances travelled were measured, and that within a clump of thistles there is much greater opportunity for vertical movement than elsewhere where the vegetation is shorter. Species of equal activity might show different horizontal displacements if in one habitat much of the time was spent in vertical movement. Furthermore, irrespective of habitat, the different sizes of the two species may also be an important factor; large snails may move further than small ones or vice versa.

Hamilton (1977, 1978), working on *Littorina irrorata* Say, emphasized the difficulty in extrapolating from short-term to long-term distances moved by animals because of the contorted nature of the paths taken. Some species of snail and slug are known to restrict their activities to rather small areas (e.g. Heatwole and Heatwole, 1978) or to return to particular areas after a period of activity (e.g. Potts, 1975; Cook 1979a, b). This may be important in the interpretation of the results for *C. virgata* and *C. intersecta* presented here, since the overnight



distances travelled are much larger than one might have expected from the results of the longer-term studies on other species quoted at the beginning of this discussion.

Greenwood (1975) considered that the long-term rate of dispersal of *Cepaea nemoralis* was inversely proportional to population density, and Cain and Currey (1968) showed that there was less emigration from areas of high population density. The work of Oosterhoff (1977) and Cameron and Carter (1979) on *Cepaea nemoralis* in captivity also showed that density could affect locomotory activity. Lamotte (1951), Cameron and Williamson (1977) and Paul (1978) have all noted the possible effects not only of overcrowding at the release point but also of disturbance due to handling and marking in mark-release studies on snails. In the present study there appear to be no effects due to overcrowding at the release point (experiments 1 and 3 compared with experiments 6 and 7 respectively). There was, however, no adequate control on disturbance since all snails were removed from the substrate in order to mark them.

The occurrence of leptokurty in the results for *C. intersecta* in 1977 (experiments 1 and 6, figs. 1a and 5a) cannot be explained without more extensive work. According to Dobzhansky and Wright (1943) a leptokurtic dispersal pattern often arises and is due to heterogeneity in the behaviour of the experimental animals. Such heterogeneity could be the result of differences in, for instance, age, reproductive or nutritional condition, morph (Altukhov and Livshits, 1978; Livshits 1978) or perhaps in a response to an environmental variable related to the weather.

Bearing in mind the limitations imposed upon this study by lack of data relating to the obtaining environmental conditions, the condition of the experimental animals, and by the difficulty of interpretation resulting from the type of experimental procedure adopted, the results do suggest that both *C. intersecta* and *C. virgata* have a high potential for rapid colonization, and for high genetic mixing within existing populations. The maximum distance moved by *C. intersecta* was similar to that quoted by Paul (1978) for the similar sized snails *Aegopinella nitidula* and *Trichia plebeia*. The larger figure for *C. virgata* may be related to this snail's larger size.

In any future, more-detailed study of this kind, it is clear that the precise details of the handling and marking procedure adopted must be carefully considered, and also that the weather conditions obtaining, age, reproductive condition and morph of the snails, habitats in which the snails are released, and length of time between release and recapture, must all be taken into account when attempting to draw any firm conclusions about the animals' capacity for dispersal.

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# WHORL NUMBER, SHAPE, AND SIZE OF SHELL IN SOME PULMONATE FAUNAS

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*Abstract:* Whorl number ( $w$ ) is only partly related to the height ( $h$ ) and maximum diameter ( $d$ ) of the shell. The distribution of  $h$  with respect to  $d$  in most faunas falls into two groups, with high-spired shells in the upper distribution (U) and equidimensional to planorboid ones in the lower (L). In French, Floridan, south-west North American and Javanese pulmonate land-snail faunas, there is little or no relation in L between  $h$ ,  $d$ , or  $h/d$  and  $w$  except that  $w$  is always low for very small shells. In contrast, the U group is highly structured with respect to  $w$ , which at high values of  $h/d$  increases very rapidly with increase in  $h$ , but falls rapidly to a rather uniform value irrespective of  $h$  as  $h/d$  decreases. It is suggested that for very slender high-spired shells a high number of whorls is necessary for mechanical strength, and for very small shells in both distributions there is a limit on the possible reduction of whorl cross-section.

In all the faunas so far examined (Cain 1977, 1978a) of fully terrestrial free-crawling stylommatophoran snails retractable into their shells, there is a bimodality of distribution of maximum shell height,  $h$ , against maximum shell diameter,  $d$ , giving an upper scatter, the U group, of tall shells with  $h$  markedly greater than  $d$ , and a lower scatter, the L group, of equidimensional to discoidal ones with  $h$  varying from approximately equal to  $d$  to much less than it. The only partial exceptions so far are the helicostyline, almost entirely Philippine, and the papuinines in New Guinea and adjacent islands, large shells which form scatters reaching from the lower part of the usual L group continuously up into the U group, although the remainder of the fauna in each region is characteristically bimodal (Cain, 1978a). Land operculate faunas in the tropics show the same bimodality everywhere except in Africa and Madagascar where they are unimodal with  $h$  approximately equal to  $d$  (Cain, 1978b). A possible ecological reason for this bimodality in the British fauna was proposed by Cain (1977) and both Cain and Cowie (1978) and Cameron (1978) have found the suggested relationship between  $h/d$  and ecological deployment, with a single species behaving anomalously in Cameron's observations.

In the investigations so far, only  $h$  and  $d$  have been considered. Dr. G. Alan Solem raised with me the question of how far variation in shape as measured by  $h/d$  is related to whorl number. A rapid check on thirteen helicostyline species in the collections of the Field Museum, Chicago, chosen to range from nearly discoidal ( $h/d = 0.5$ ) to high-spired ( $h/d = 2.5$ ), produced the rather surprising result that whorl number varied only from 4 to 6, and was therefore only slightly associated with  $h/d$ , at least in these species.

Since helicostyline do not become as tall and slender as several other groups of land-snails (clausiliids, urocoptids, subulinids etc.) and to check variation of  $h/d$  with  $w$  in faunas with species bimodally distributed as usual, faunas in three different zoogeographical regions were investigated. The present paper gives the results of this work and suggests some reasons for them.



## MATERIALS AND METHODS

The data given by Germain (1930) were used as representative of a European fauna, introduced forms, semi-slugs, slugs, and dubious species being excluded. In previous papers I used only fully terrestrial forms; a review of species characterized by Germain as 'hygrophil' showed only forms fitting well into the known scatters, and they have therefore been used also. Since the Succineidae, although amphibious, do spend time out of water (and some tropical ones are terrestrial) they have also been included in the survey but symbolized differently – in fact they seem to introduce no anomaly into the results.

To test the generality of the findings from the French fauna, surveys were also made of two fairly rich and taxonomically different North American faunas, those of Florida and of California plus Arizona, using Pilsbry's *Monograph* (1939–1948). Lastly, the Javanese fauna was looked at in van Benthem Jutting's excellent papers (1977) supplemented by those of Loosjes (1953, 1963, 1965) for the clausiliids.

## RESULTS

Fig. 1 shows the data from Germain for the French fauna, plotted as  $h/d$  (ordinate) against whorl number (abscissa), to find out how far shell shape depends on whorl number. Species of the U group are shown as solid black circles except for a single decollate form (*Rumina decollata*, circle with central spot); succineids are shown by triangles. Species of the L group are shown as open circles. A single species of *Helix*, the rest of which undoubtedly belong to the L group, is at  $h/d = 1.2$ ,  $w = 4$  (*Helix aperta*). A diagram of  $h$  against  $d$  for the fauna is given by Cain (1977, fig. 3) and, symbolized for whorl number in Fig. 6, below. The lowest black circle is for *Cochlicella conoidea* which is intermediate between the two groups.

Germain gives ranges for whorl number, using only whole numbers (e.g. 7 to 9) or large fractions (e.g.  $4\frac{1}{2}$  to 5), so that the data tend to clump on the ordinates. Nevertheless, there is sufficient variation to give a reasonable picture of the relationship between  $h/d$  and  $w$ .

It is clear first of all that there is no relationship between  $w$  and  $h/d$  in the L group, ( $h/d =$  about 1 or less) whereas there is a strong one in the U group; and the succineids, which on their values of  $h/d$  certainly belong to the U group, fit in well with it. What is happening at intermediate values of  $h/d$  (1.1 to 1.5) is uncertain because this region corresponds to the gap between the two groups. There are only two points in it, which make no difference to the result whichever way they are allocated. For any given whorl number there is a wide variation of  $h/d$ , and the helicostylines originally observed would merely reinforce the present diagram if added to it. In fact, if it were not for the succineids, one might well consider that the lower part of the upper scatter in Fig. 1 from  $h/d = 2.5$  (or thereabouts) downwards is simply an upward extension of the lower scatter, and equally without any relation between  $h/d$  and  $w$ . With the succineids, however, it seems better to take the whole of the upper scatter as a homogeneous distribution.

The marked difference between the upper and lower scatters requires further investigation. In figs. 2 and 3,  $w$  is plotted for the L group against  $h$  and against  $d$ . There is some indication that  $w$  is low for very low values of both  $h$  and  $d$ , but otherwise there is no relation between them. Figs. 4 and 5 give the same plots for the U group, and a strong relation can be seen between  $w$  and  $h$ , a lesser one between  $w$  and  $d$ , for the majority of points but not for the succineids nor for the decollate form and two or three others.

These diagrams suggest some heterogeneity of relations between  $w$ ,  $h$  and  $d$  in the two groups. Accordingly, in fig. 6, the standard diagram for this fauna of  $h$  against  $d$  is plotted but symbolized for whorl number. (To allow for clear symbols, the scale is large, and a few species are off the diagram, but do not disturb the trends shown). This diagram shows no relations in the lower scatter, except that the smallest shells do seem to have a lower mean value of  $w$  than the



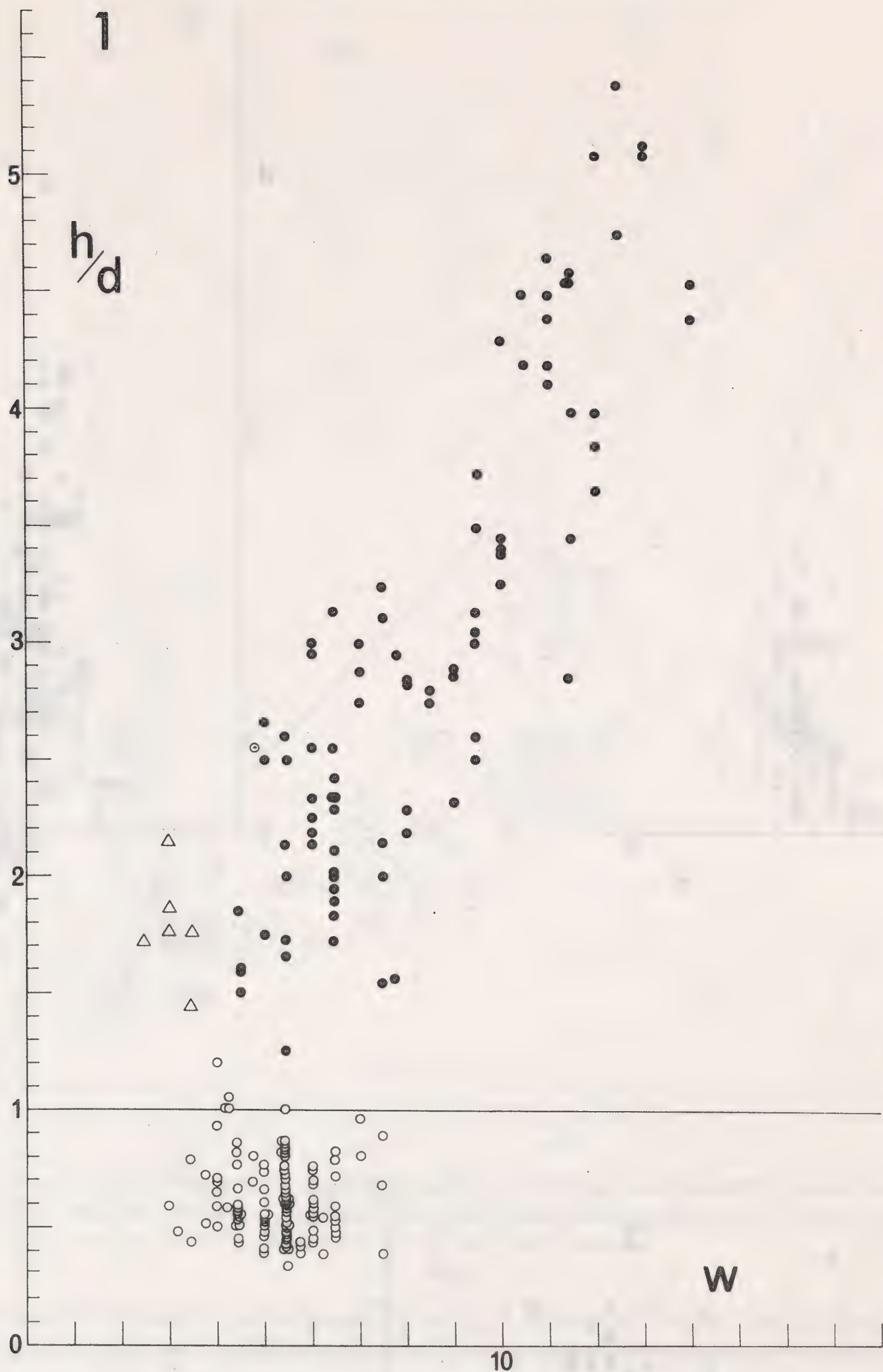


Fig. 1. Scatter-diagram for  $h/d$  (ordinate) against  $w$  (abscissa) for the French terrestrial pulmonate fauna. Open circles, species belonging to the L group. Black circles, species belonging to the H group. Circle with central dot, *Rumina decollata* (decollate). Triangles, succineids.

rest. The upper scatter, however, is highly structured. There is a marked increase in whorl number with  $h$  amongst those shells with a high value of  $h/d$ , i.e. along the edge of the scatter nearest the ordinate axis, but at each value of  $h$ , at least above  $h = 5$ , there is a very rapid decrease in whorl number with increase in  $d$ . With the lowest value of  $h/d$ , i.e. along the occupied radius nearest the bisector, whorl number is very low and does not increase with increase in  $h$ . (These are the succineids.)



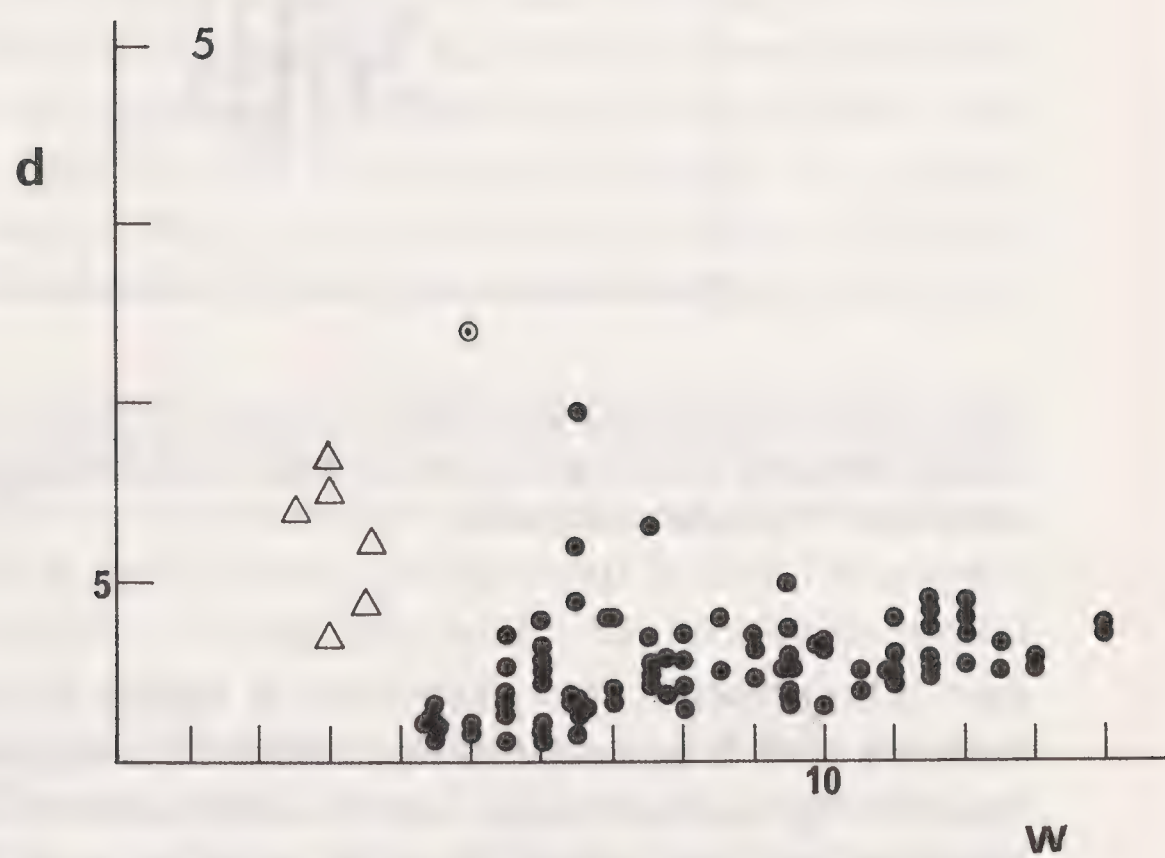
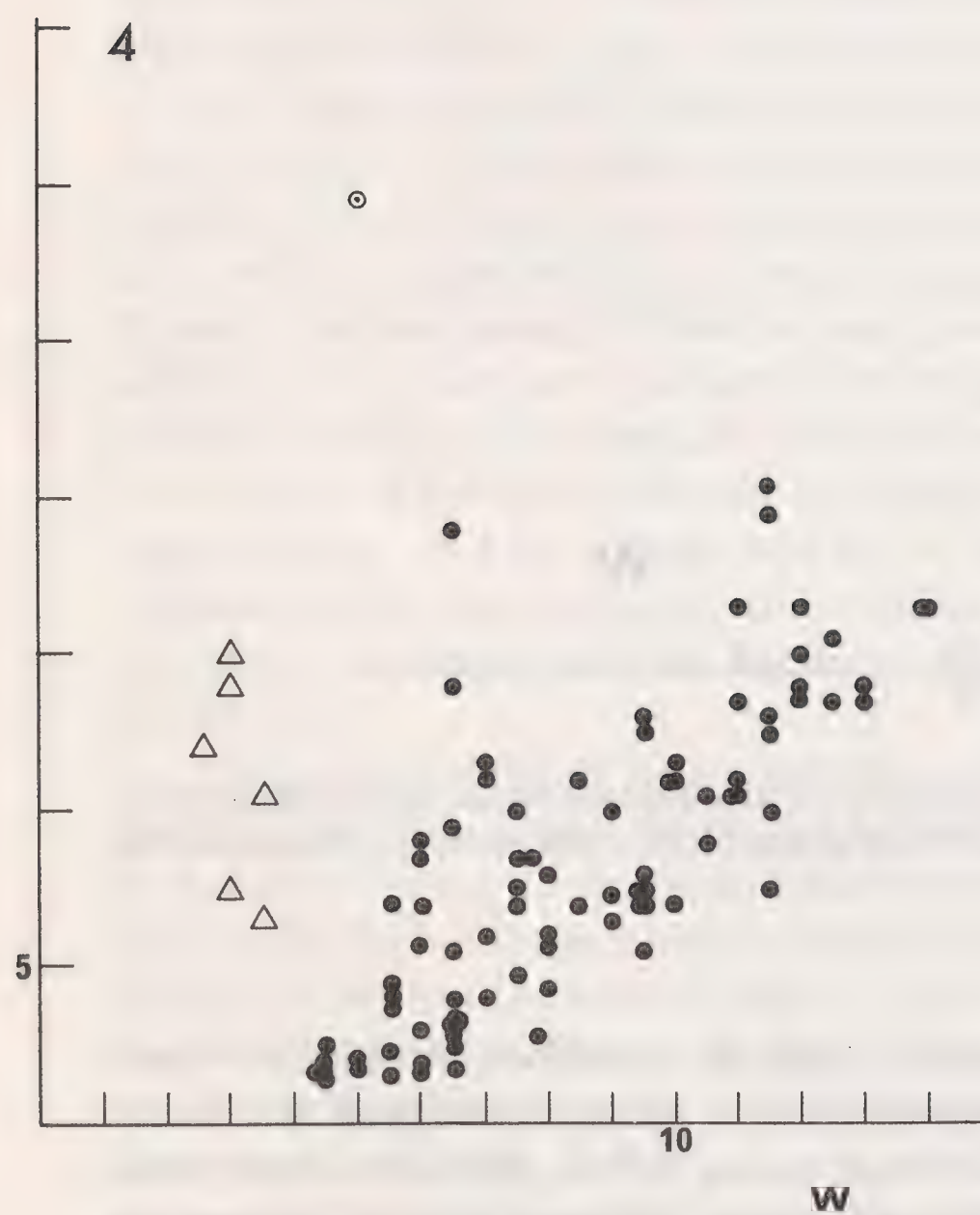
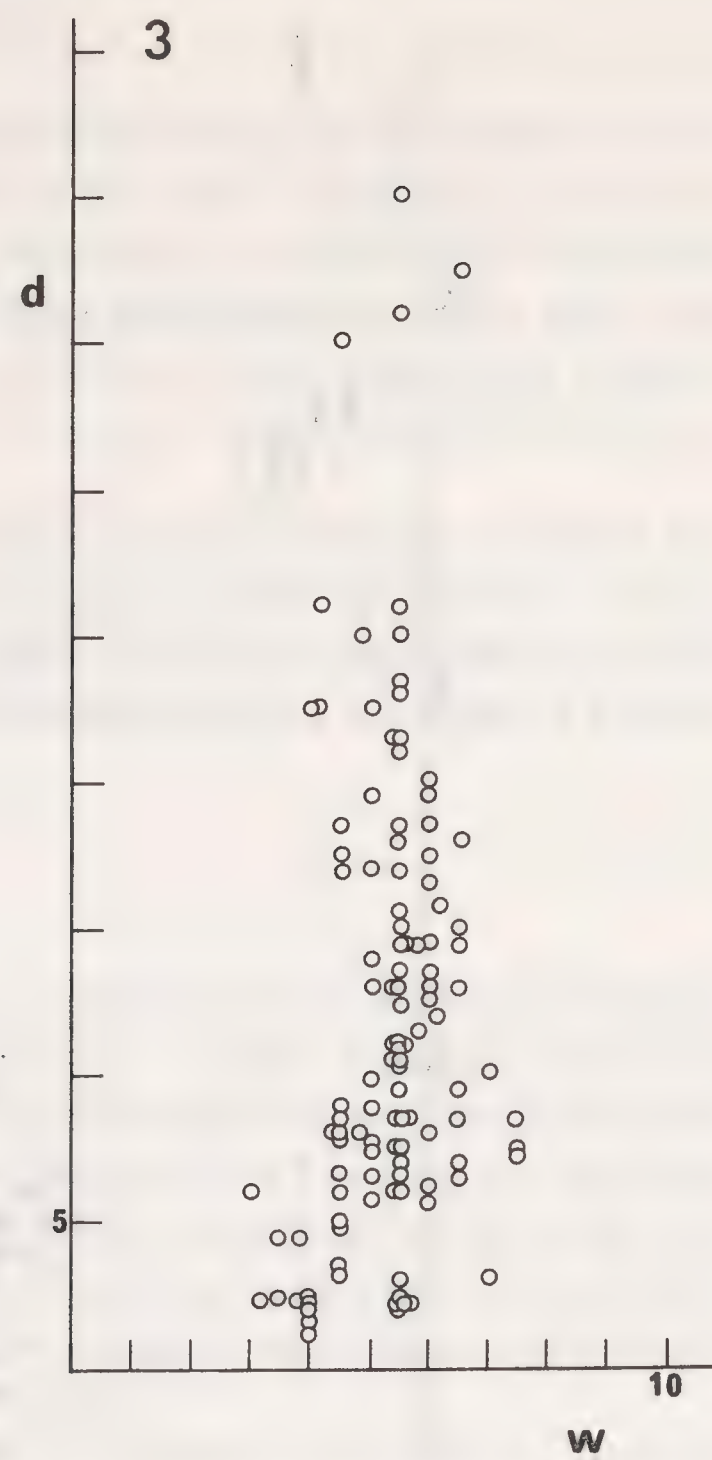
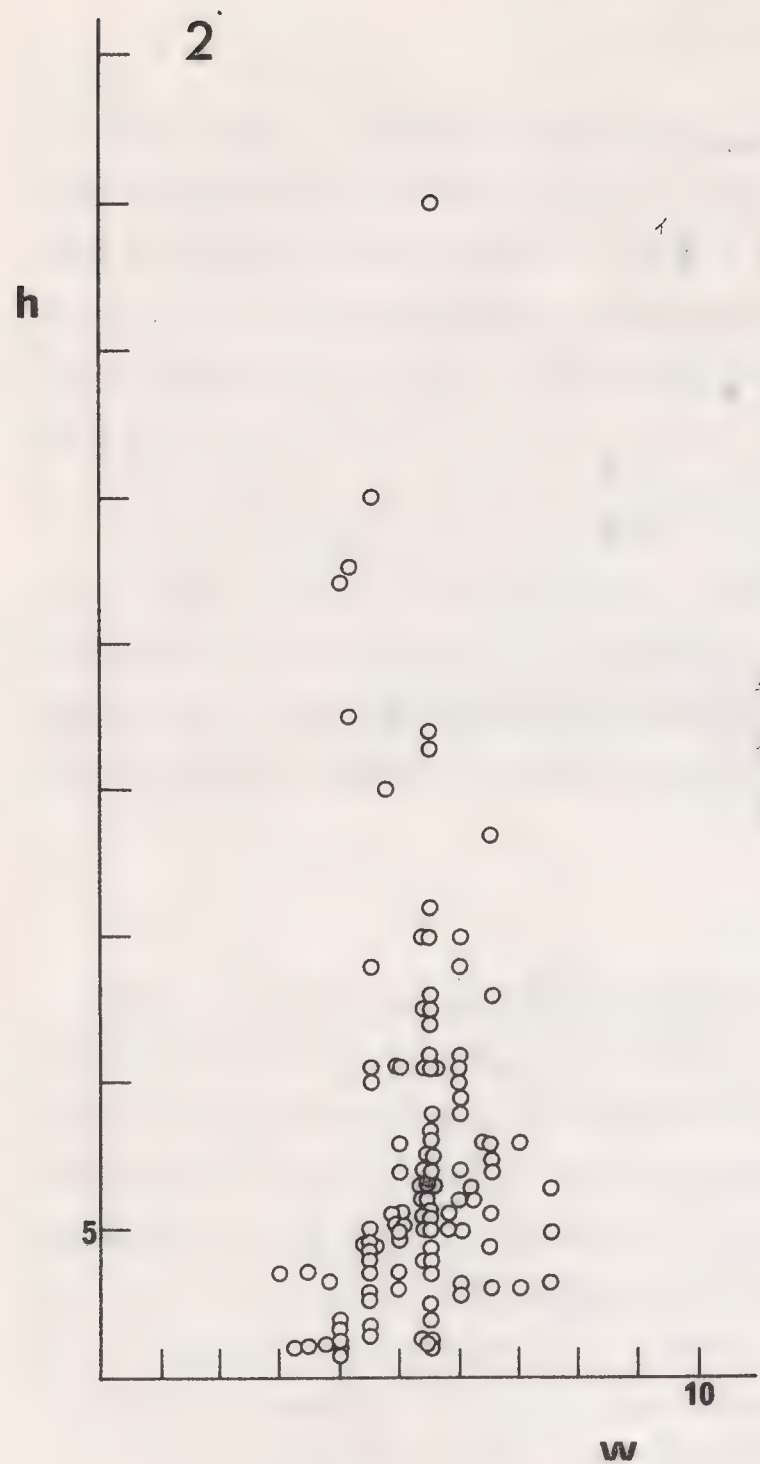


Fig. 2. French fauna, L group; h (ordinate) against w (abscissa). Fig. 3. French fauna, L group; d (ordinate) against w (abscissa). Fig. 4. French fauna, U group; h (ordinate) against w (abscissa). Fig. 5. French fauna, U group; d (ordinate) against w (abscissa).



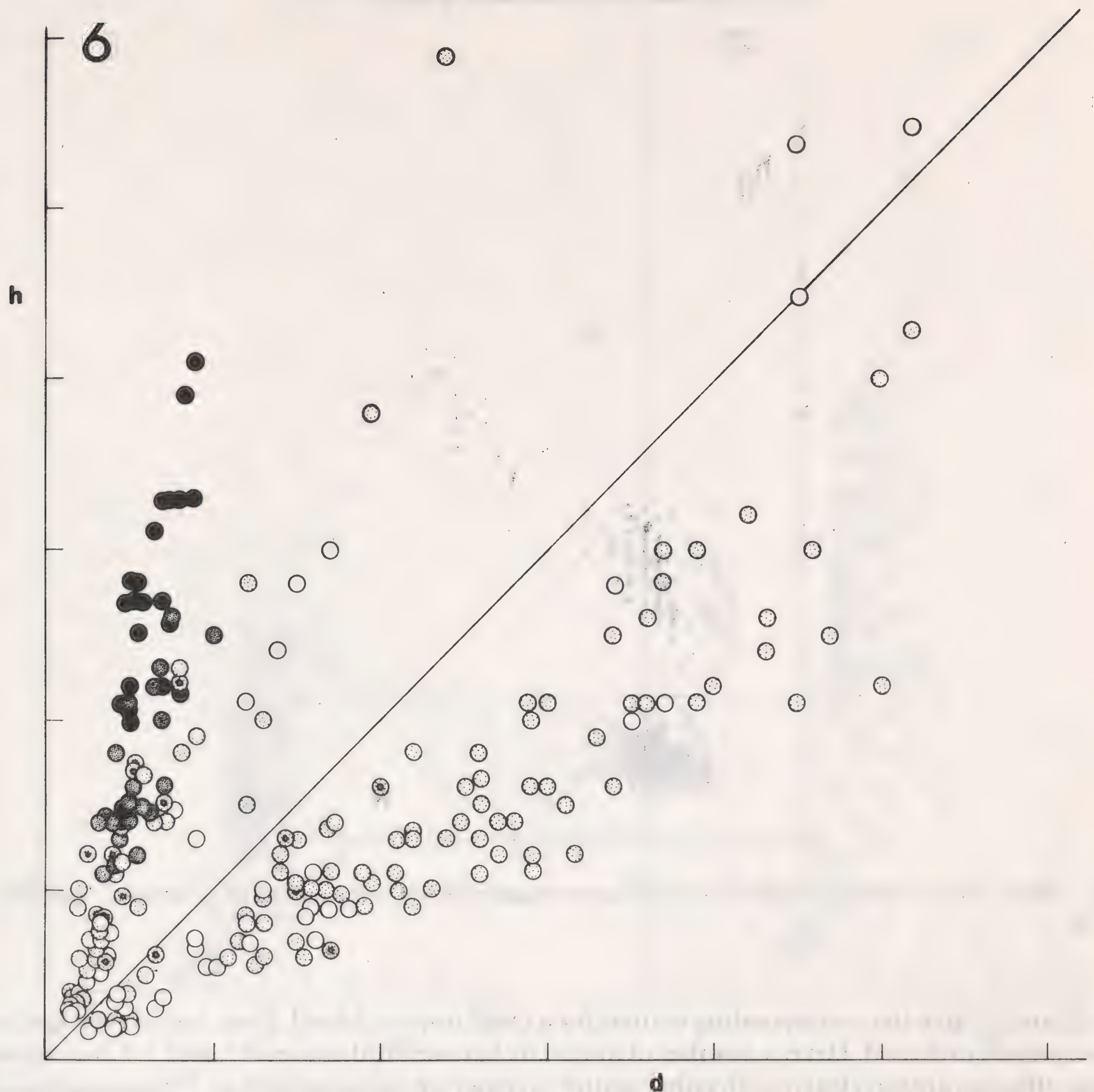


Fig. 6. French fauna, scatter diagram for  $h$  (ordinate) against  $d$  (abscissa) symbolized for whorl number,  $w$ . Open circles,  $w$  2-4; lightly stippled circles,  $w$  5-7 (those with value 7 have a clump of dots at the centre); heavily stippled circles,  $w$  8-10; black circles,  $w$  11-14. Both axes marked at 5 mm intervals.

The diagram of  $h/d$  and  $w$  corresponding to fig. 1 (France) for the North American fauna is given in fig. 7, and confirms the findings from fig. 1, although there are few families, few genera, and almost no species in common (introduced species being left out). Also, the regression of  $h/d$  on  $w$  in the U group is less steep than in fig. 1. The North American fauna being geographically diverse, two regions were selected for direct comparison with the French fauna; figs. 8 to 11 give the corresponding plots of  $w$  against  $h$  and  $d$  for California and Arizona combined, and fig. 12 the  $(h, d)$  scatter symbolized for  $w$ . Figs. 13 to 16, and 17 do the same for Florida. In both regions the prevalence of low  $w$  with low  $h$  and  $d$  is confirmed in the L group, and the same type of heterogeneity as before is found in the U group. In the Florida U group, the non-succineids not varying in shape and size with whorl number are much better represented (fig. 15 and 16) than in the French or the California-Arizona faunas, while those that are closely related to whorl number are better represented in the French than in either of the North American regions. Adding the Texan fauna (which is also of eastern North American type although with peculiarities of its own) to the Floridan simply thickens the scatters already seen. Lastly, figs. 18



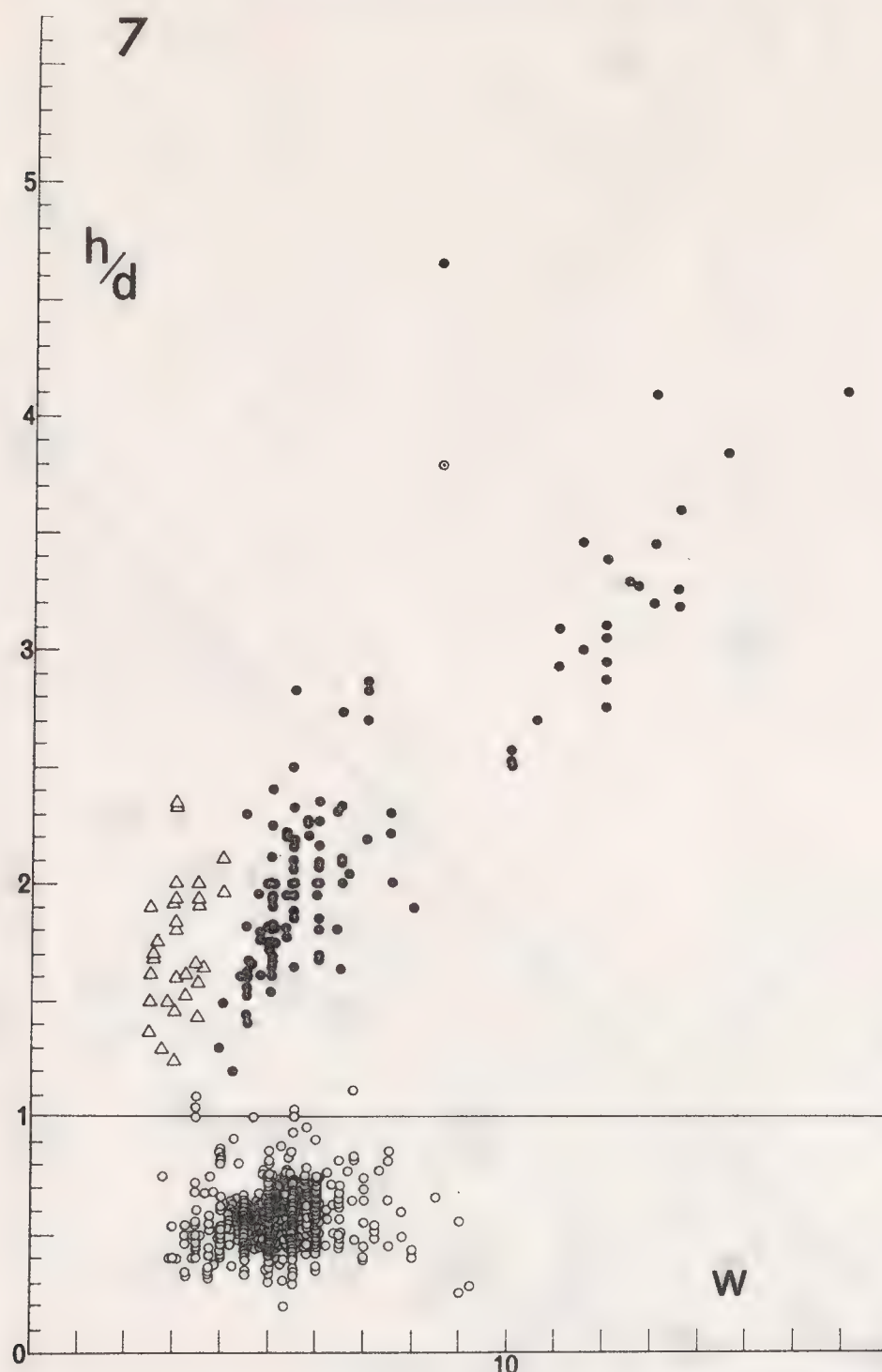


Fig. 7. North American terrestrial pulmonate fauna; scatter diagram for  $h/d$  (ordinate) against  $w$  (abscissa). Symbols as in fig. 1.

to 22 and 23 give the corresponding scatters for a large tropical island, Java, introduced species being again excluded. Here, a number of species lie between  $h/d$  values of 1 and 1.2, but again, their affinities are not clearly with either scatter in respect of variation with  $w$ . The association of  $w$  with  $h$  for very high values of  $h/d$  is less regular here (fig. 23) but the general pattern is the same. The regression of  $h/d$  on  $w$  is the steepest of the three.

#### DISCUSSION

The distributions of  $h/d$  and  $w$  shown in figs. 1, 7 and 18 seem to be characteristic of land pulmonates in general, judging from the illustrations in Zilch (1959–1960). Almost all the species figured there would merely thicken the scatters for both the U and L groups. Very tall shells have evolved independently several times; such forms as *Bostryx* (*Geoceras*) *columellaris* (Reeve) (Bulimulidae;  $h/d = 4.64$ ,  $w = 17$ ), *Hemiphaedusa* (*Tyrannophaedusa*) *mikado* (Pilsbry) (Clausiliidae Phaedusinae;  $h/d = 6.4$ ,  $w = 19$ ) or *Epirobia* (*Epirobia*) *polygyra* (Urocoptidae Eucalodiinae;  $h/d = 7.0$ ,  $w$  about 23) simply prolong the upper scatter in fig. 1 upwards. Even *Prosopeas* (*Paropeas*) *acutissimum* (Mousson) (Subulinidae Subulininae;  $h/d = 5.59$ ,  $w$  about 11) *Cerion incanum* (Binney) (Ceriidae;  $h/d = 2.38$ ,  $w = 10.5$ ), or *Placostylus* (*Eumecostylus*) *cleryi* (Petit) (Bulimulidae;  $h/d = 3.34$ ,  $w = 6$ ), although slightly peripheral, probably belong to it. *Quickia concisa* (Morelet) (Succineidae;  $h/d = 1.625$ ,  $w$  only 2.5) prolongs it downwards and to the left as might be expected for a succineid. Only three genera produce definitely exceptional forms. These are *Megaspira* (Megaspiridae), *Columna* (Achatinidae) and *Ganesella* (Camaenidae).



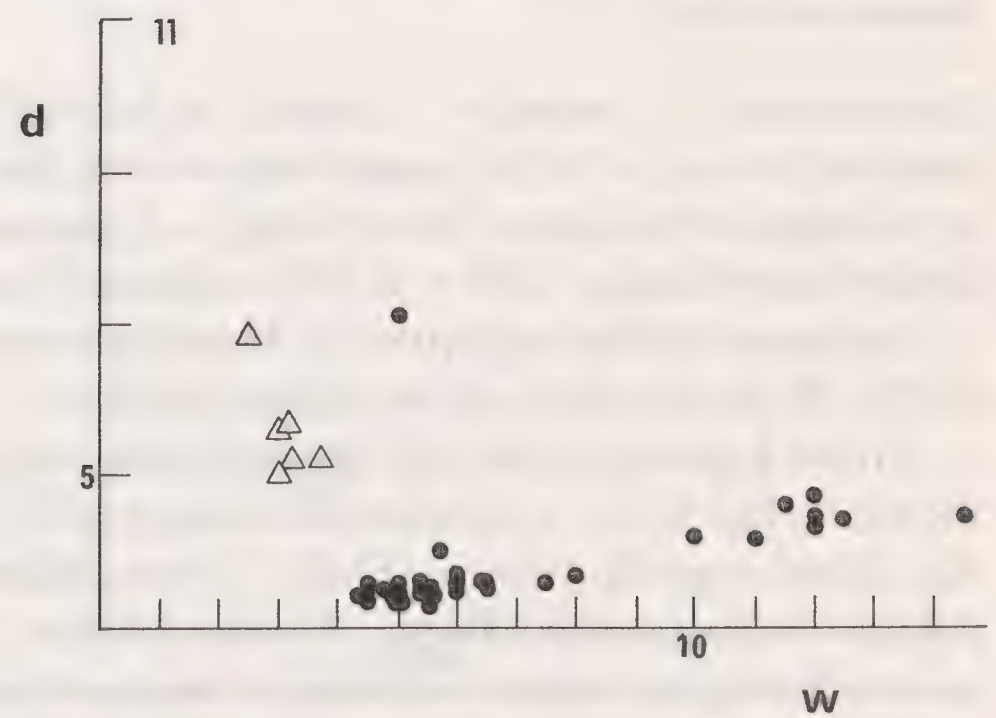
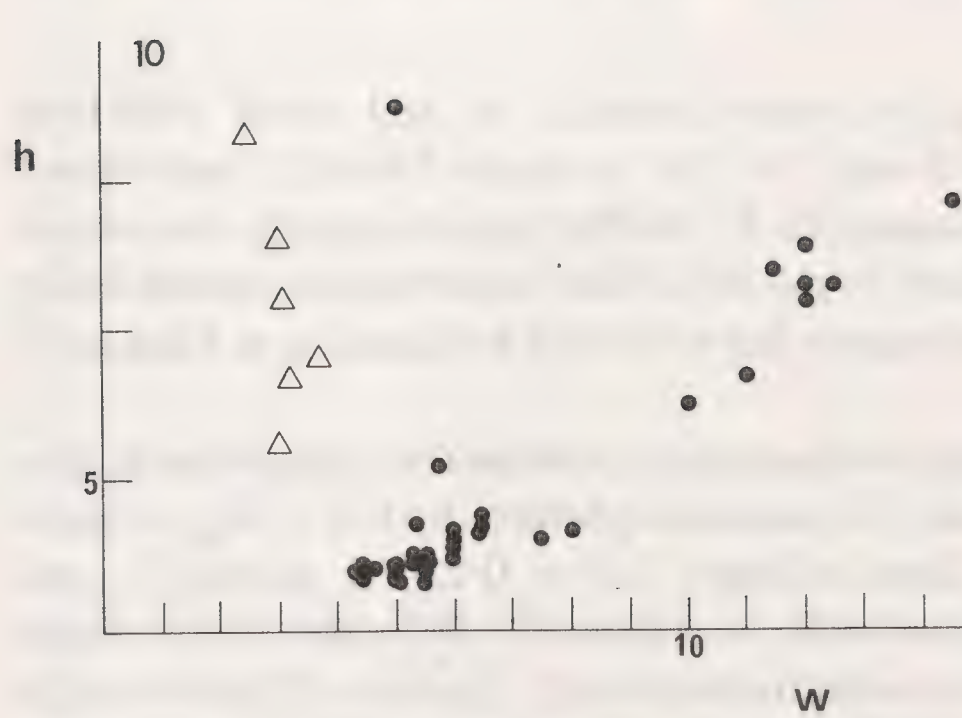
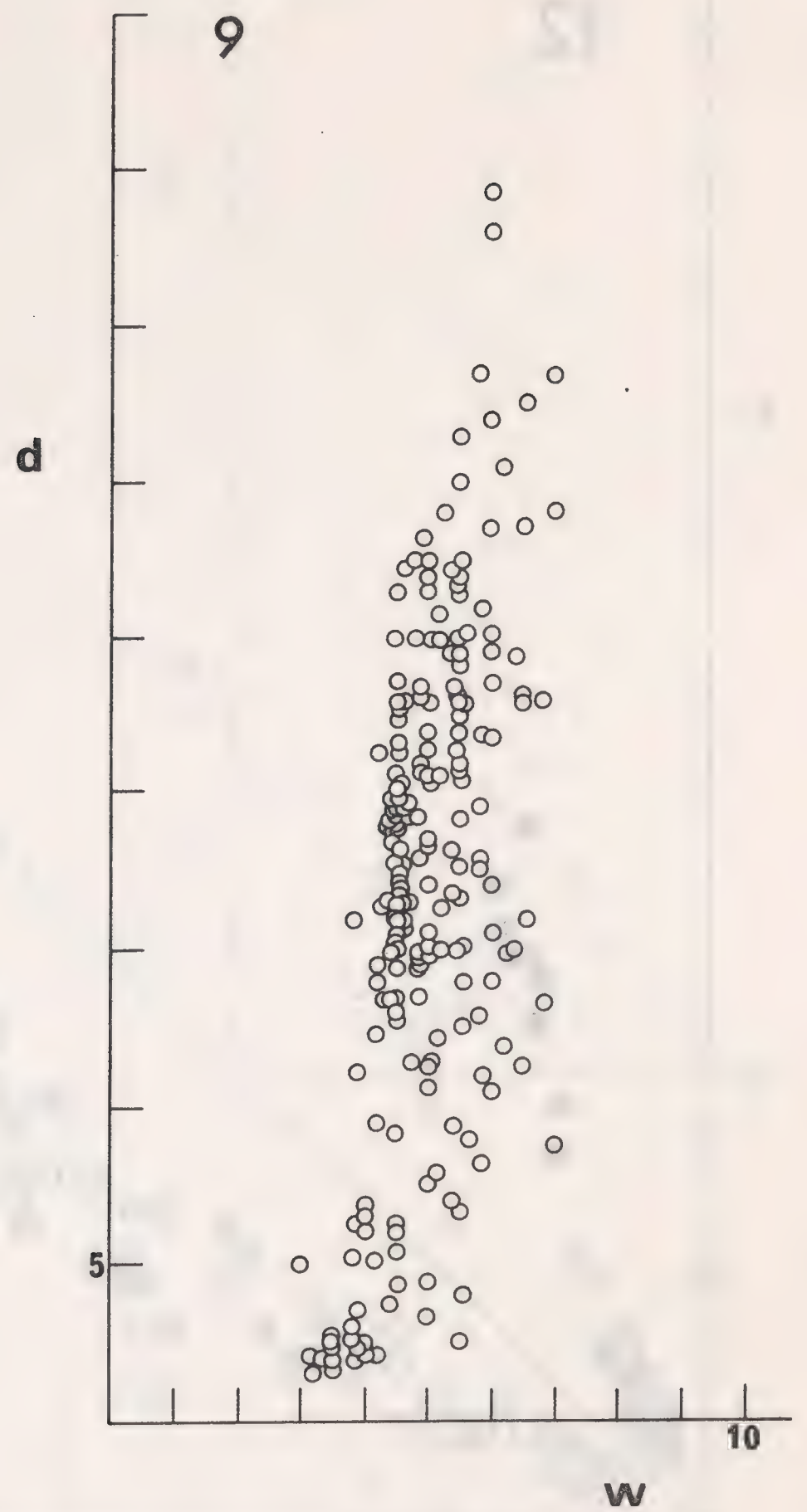
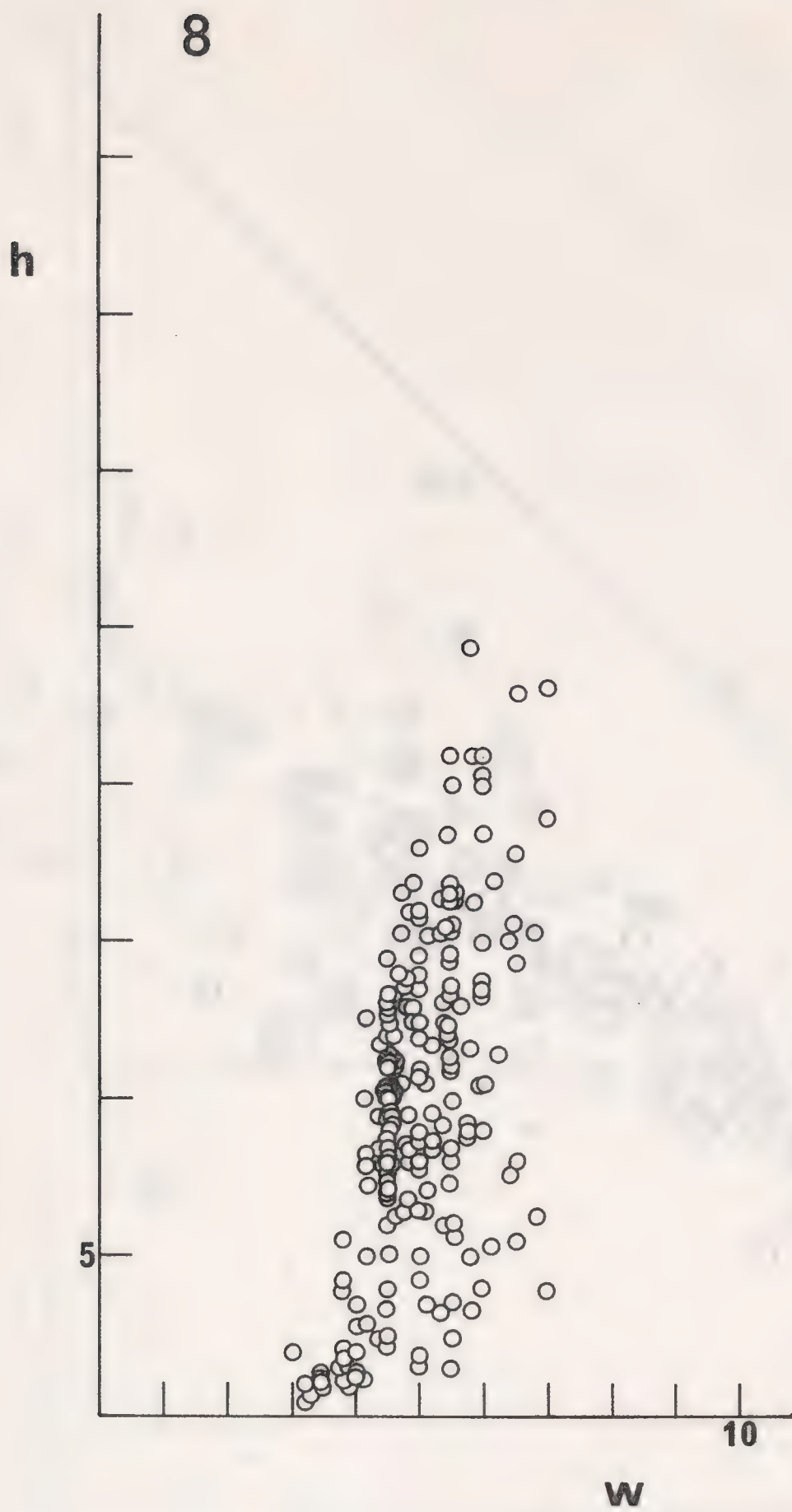


Fig. 8. California-Arizona fauna, L group;  $h$  (ordinate) against  $w$  (abscissa). Fig. 9. California-Arizona fauna, L group;  $d$  (ordinate) against  $w$  (abscissa). Fig. 10. California-Arizona fauna, U group;  $h$  (ordinate) against  $w$  (abscissa). Fig. 11. California-Arizona fauna, U group;  $d$  (ordinate) against  $w$  (abscissa).



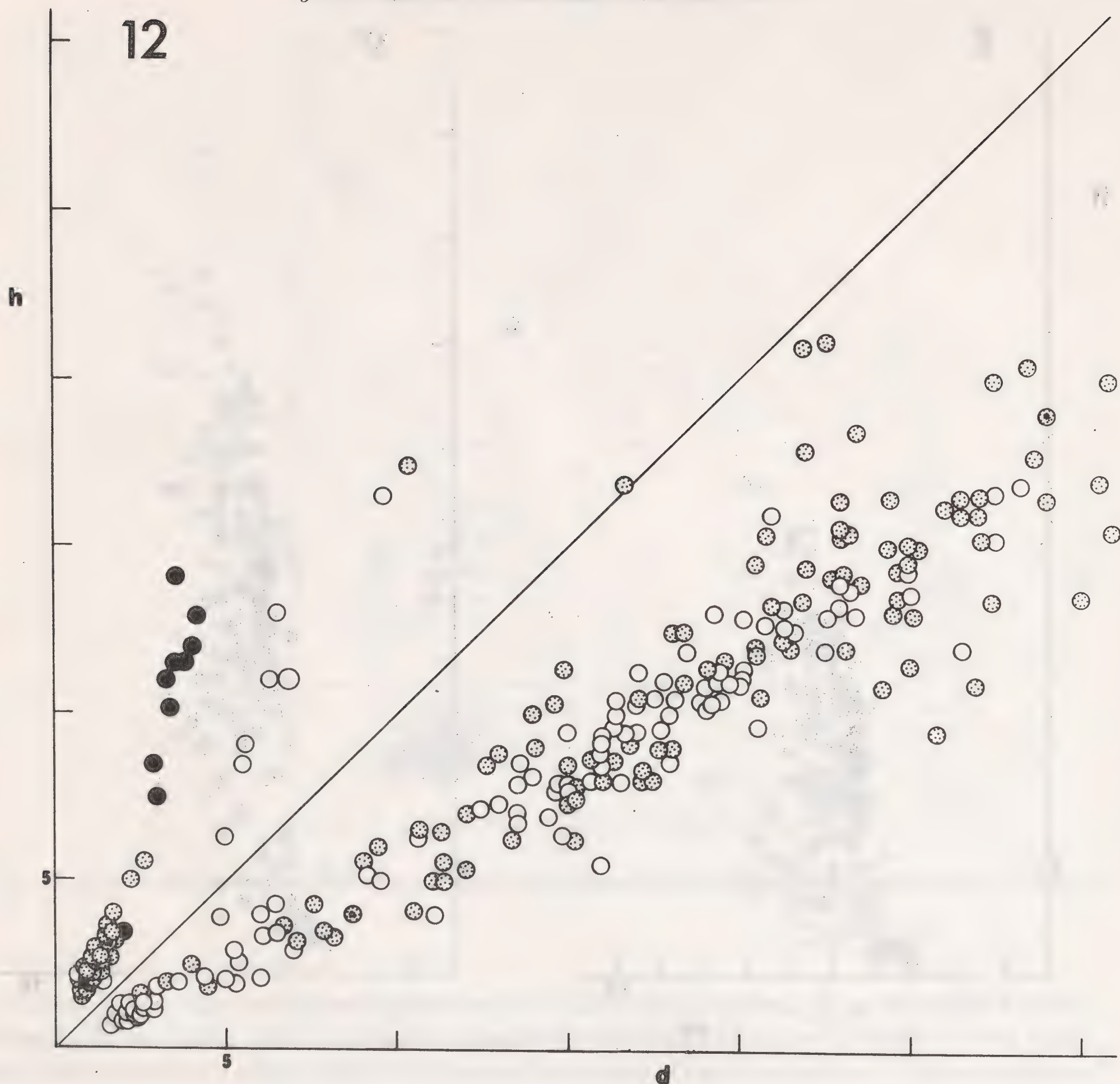


Fig. 12. California-Arizona fauna; scatter diagram for  $h$  (ordinate) against  $d$  (abscissa), symbolized for whorl number. Symbols as in fig. 6.

Camaeninae). *Ganesella (Coliulus) arfakiensis* (Tapparone-Canefri), a tall form widening extremely rapidly to the broad body-whorl, has  $h/d$  only 1.41 but  $w$  about 10 or 11, and sits out to the right of the upper scatter in fig. 1. *Columna columna* (O. F. Müller) has markedly few whorls for its slender shape ( $h/d = 5.303$ ,  $w$  about 8) and sits to the left of the uppermost symbols in fig. 1. The most marked exception is *Megaspira ruschenbergiana* Jay with  $h/d$  4.61 and  $w$  as high as 21 or 22, far to the right of the upper scatter.

In the L group, a few very flat and many-whorled shells can be added to the right of the scatter shown in fig. 1, for example *Coxia macgregori* (Cox) (Trochomorphidae;  $h/d = 0.29$ ,  $w$  about 10), *Hendersoniella palmeri* (Dall) (Urocoptidae Eucalodiinae;  $h/d = 0.23$ ,  $w$  about 9), and *Polygyratia polygyratia* (Born) (Systrophiidae;  $h/d = 0.26$ ,  $w$  about 9). Whether these forms extend the lower scatter to the right and downwards needs further study. Species of *Polygyra* seem to do so in the North American fauna (fig. 7). Otherwise, the scatter in fig. 1 seems representative for equidimensional to flat shells generally. (Shells with fewer whorls, down to nearly 0, which would be a perfectly flat plate, do occur on the left-hand side of the lower scatter but belong to semi-slugs or slugs, which are not considered here).



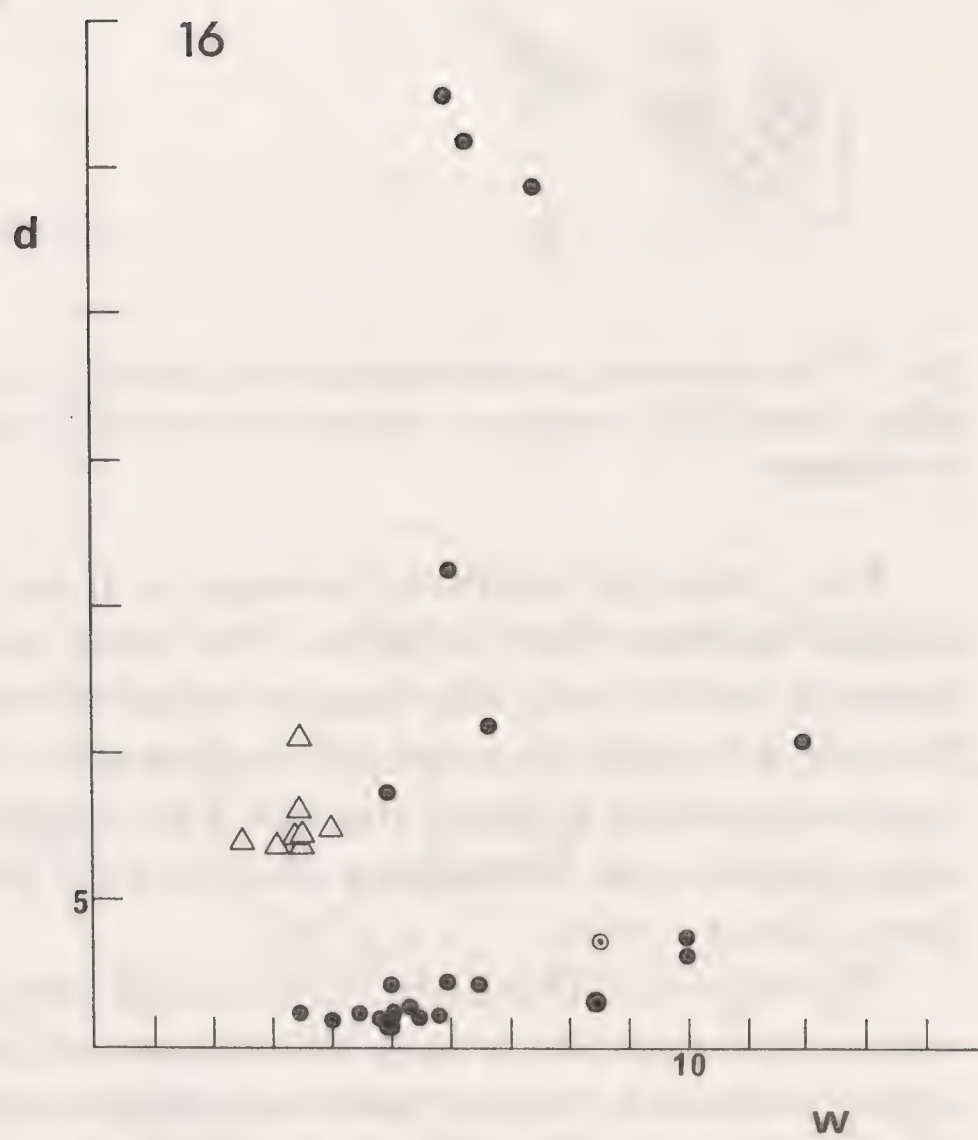
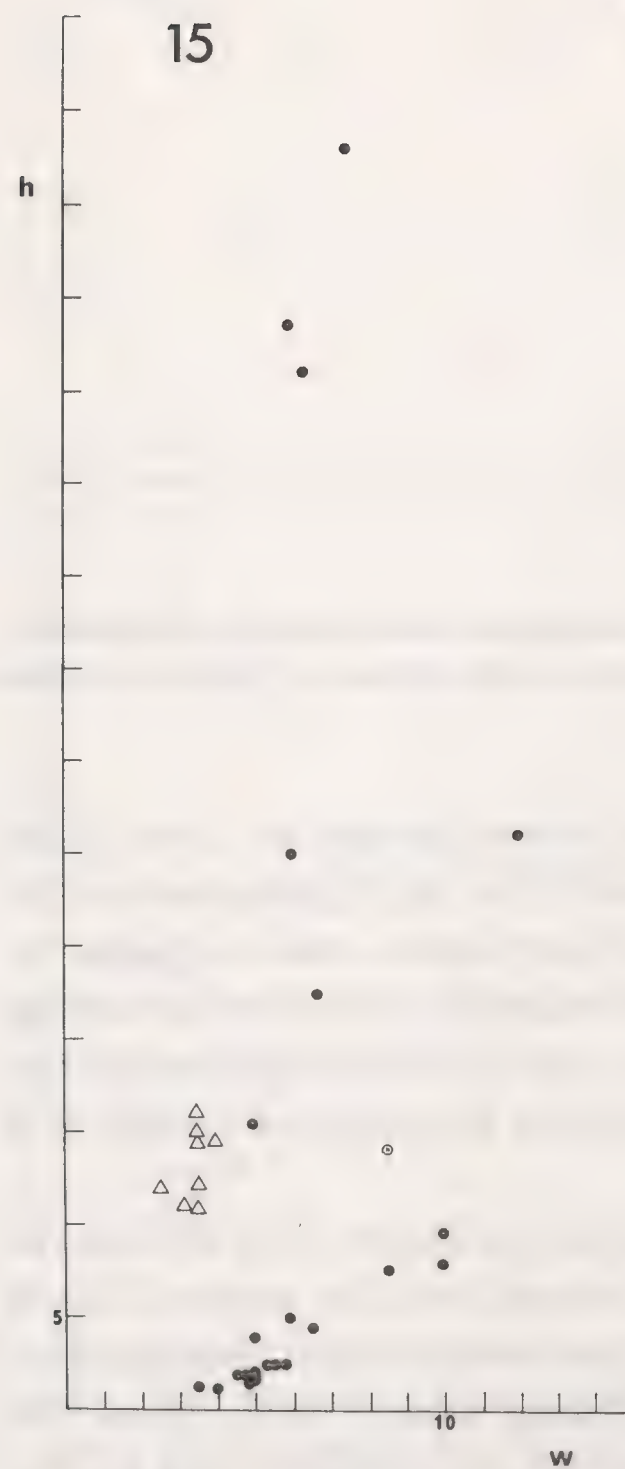
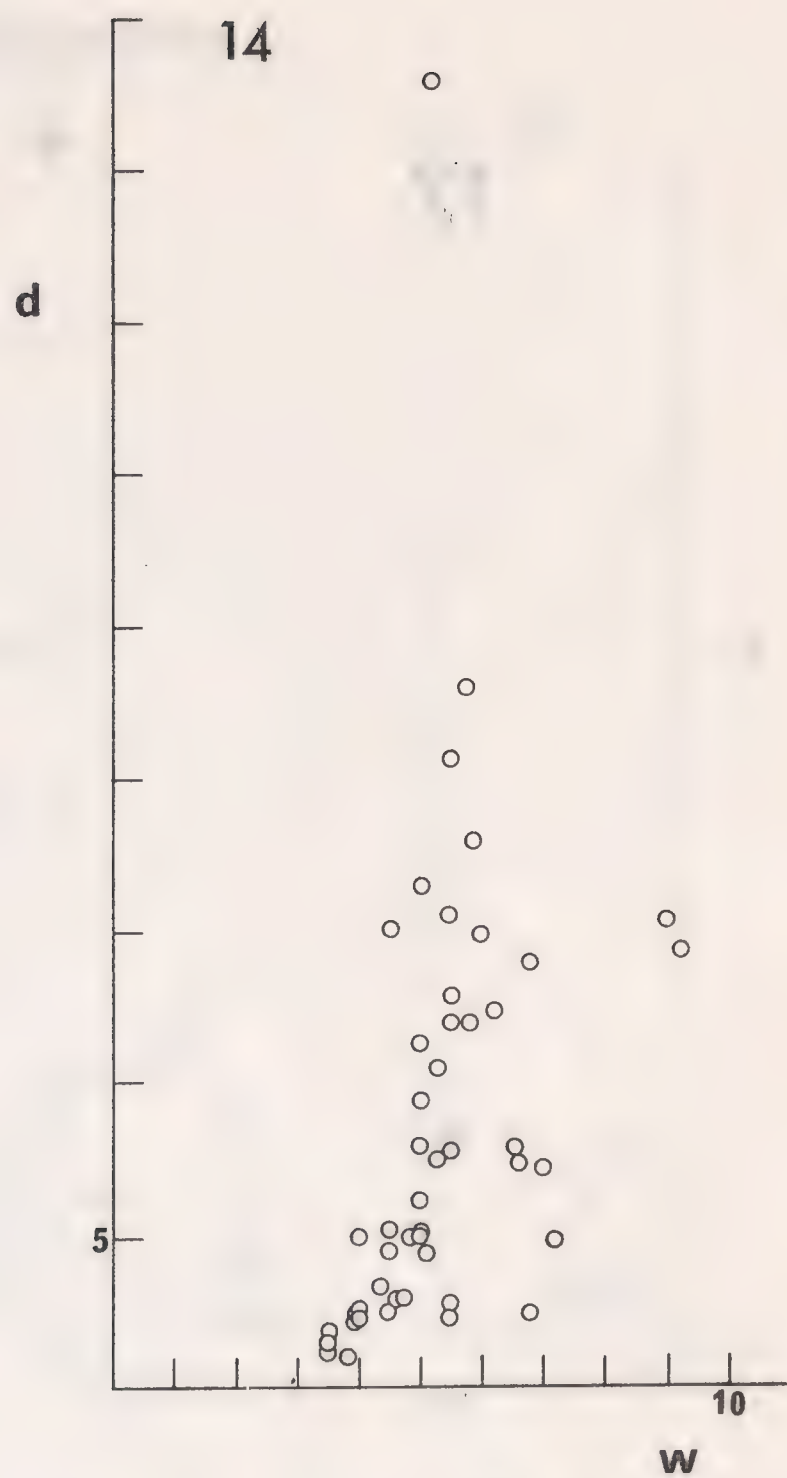
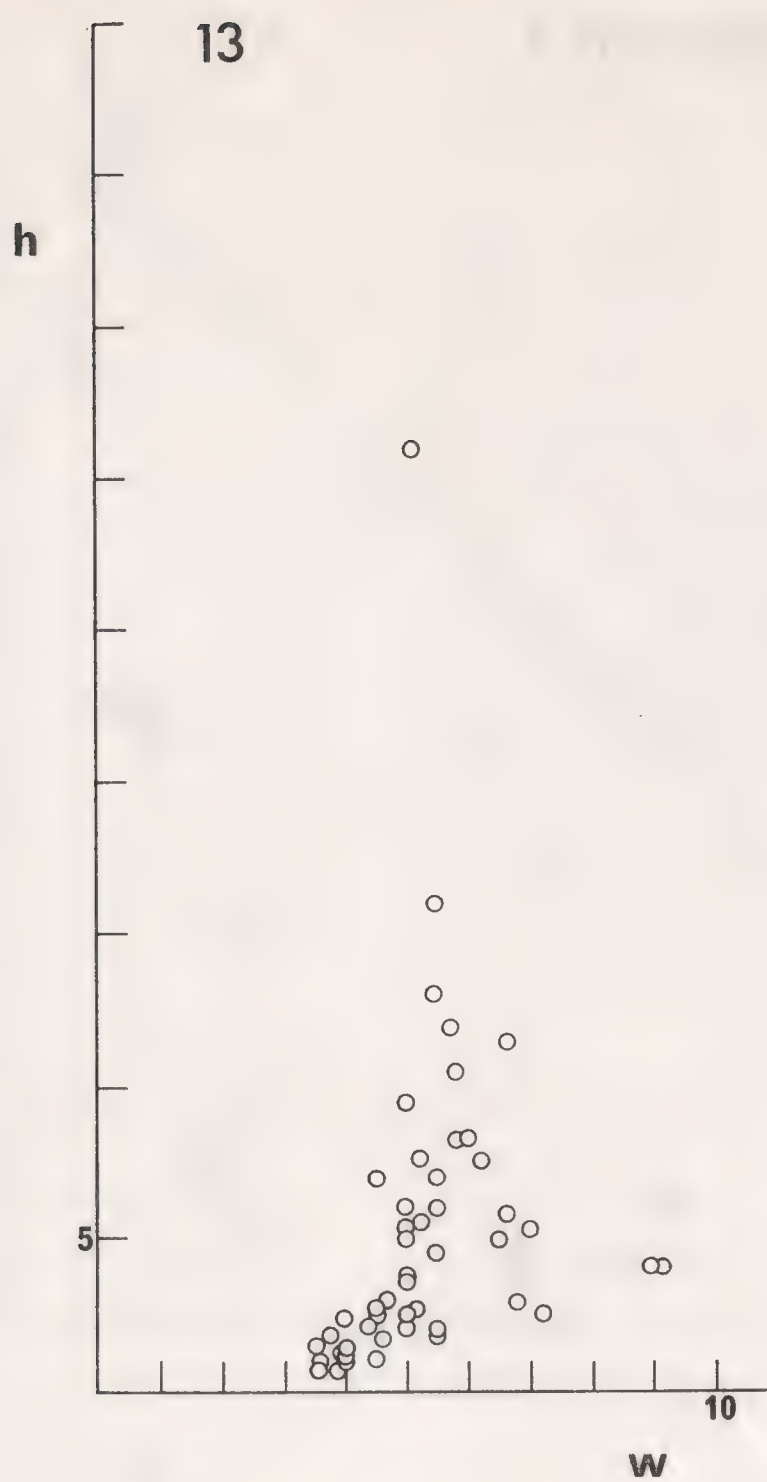


Fig. 13. Florida fauna, L group; h (ordinate) against w (abscissa). Fig. 14. Florida fauna, L group; d (ordinate) against w (abscissa). Fig. 15. Florida fauna, U group; h (ordinate) against w (abscissa). Fig. 16. Florida fauna, U group; d (ordinate) against w (abscissa).



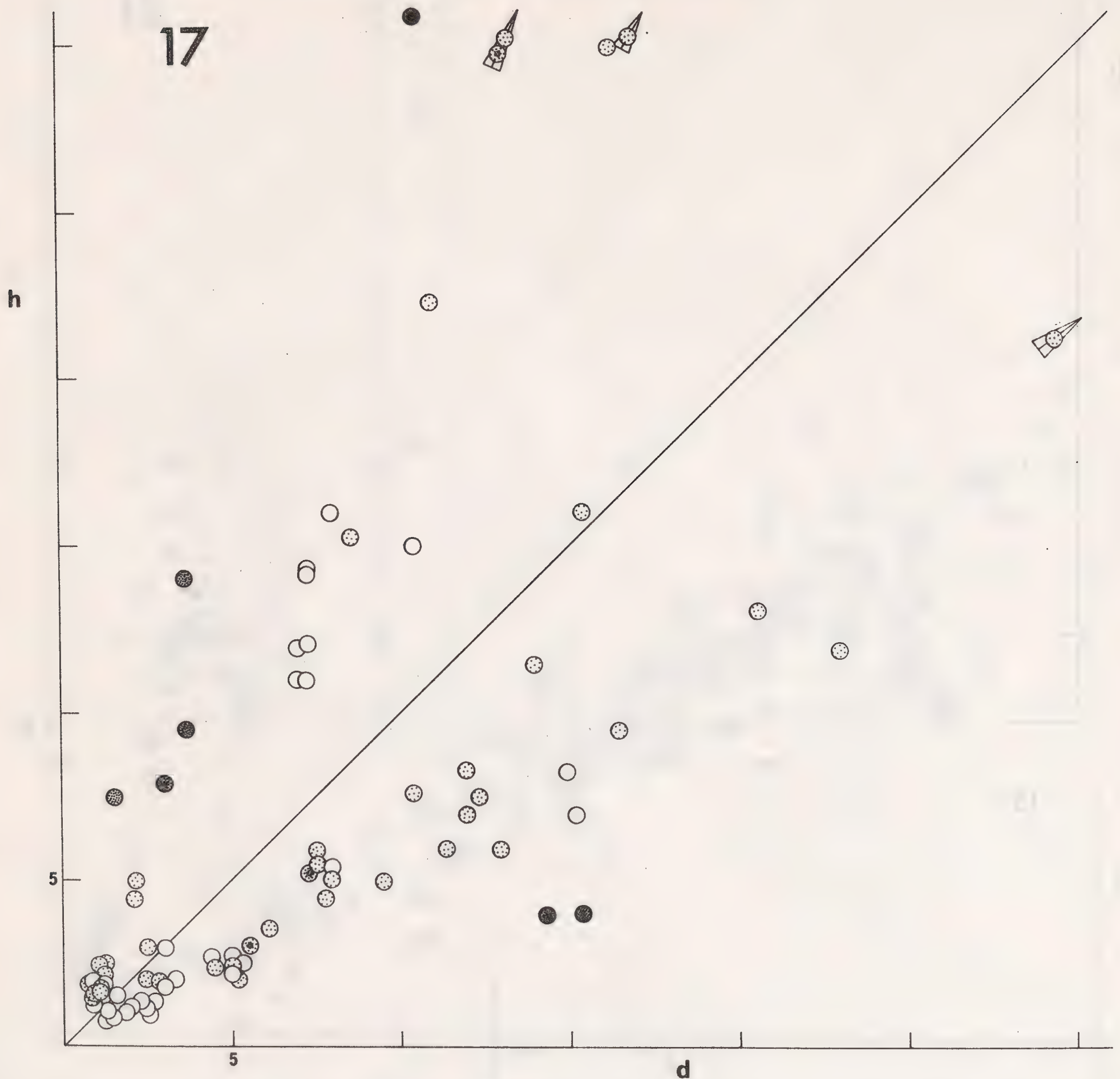


Fig. 17. Florida fauna; scatter diagram for  $h$  (ordinate) against  $d$  (abscissa), symbolized for whorl number. Symbols as in figs. 6 and 12. Pointers carry appropriate symbols for, and point in the direction of, a few species too large to go into the diagram.

Two principal relations between  $w$ ,  $h$  and  $d$  emerge from the results just given. One is the obvious tendency for  $w$  to be low (4 or often less) in figs. 6, 12, 17 and 23 in the L group when  $d$  is 3 mm or less; this can also be seen in the corresponding scatters of  $h$  against  $w$  and  $d$  against  $w$ . There is a hint of the same phenomenon in the U group as well. Secondly, there is the strong structuring of the U group in respect to  $w$  and  $h/d$ , best seen in fig. 1 but certainly present in the other faunas, and contrasting sharply with the lack of structure in the L group for values of  $d$  above about 4 mm.

The reduction in number of whorls in very small shells of the L groups means that the area of internal cross-section of each whorl taken at any given number of whorls from the nepionic shell is proportionately larger than it would have been if all shells had (say) seven whorls irrespective of size. It is possible that there is a minimum cross-sectional area which will allow the haemocoelomic fluid to flow freely both to allow the animal to retract and expand and for the proper respiratory and other functions of the blood. If the internal organs were very closely



# SOME PULMONATE FAUNAS

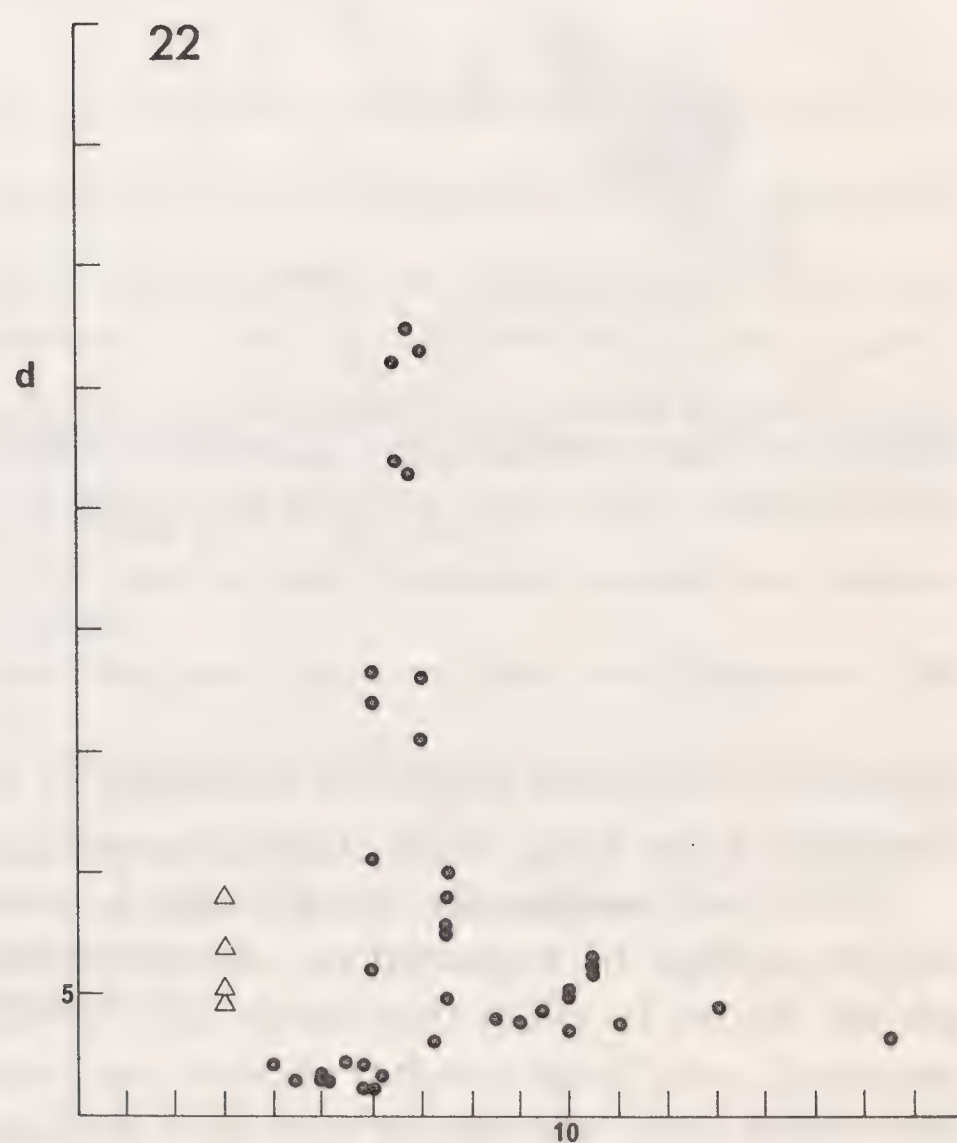
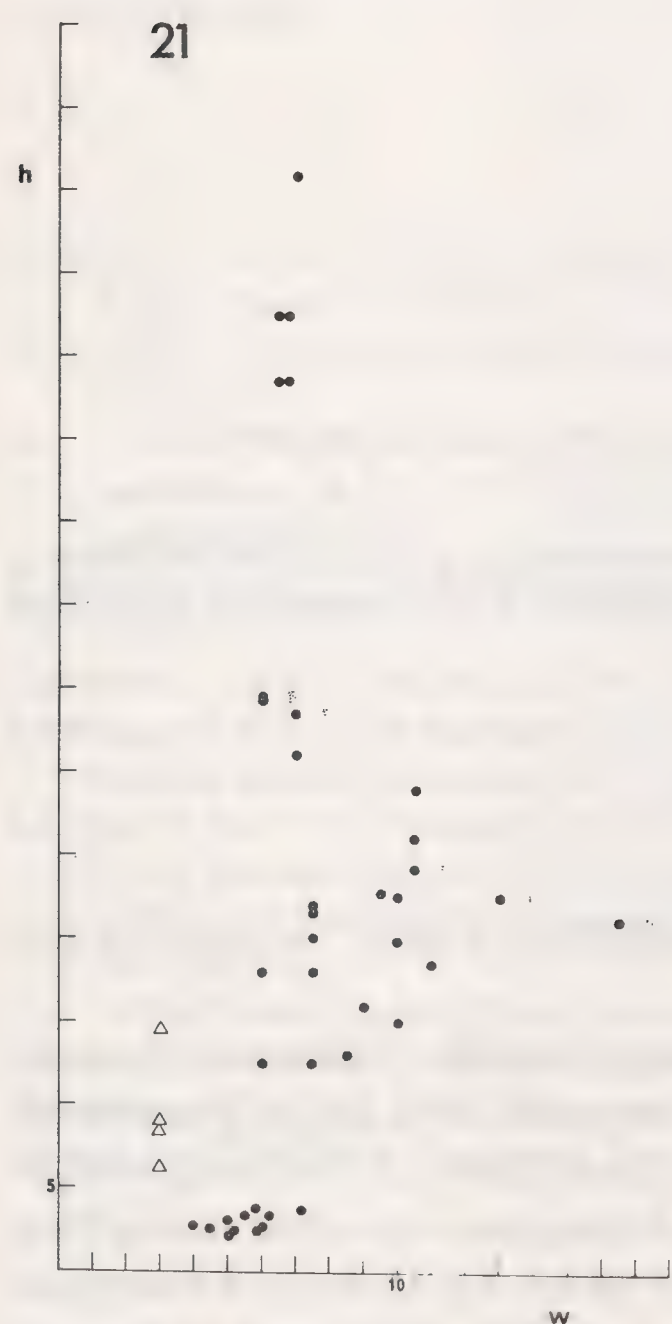
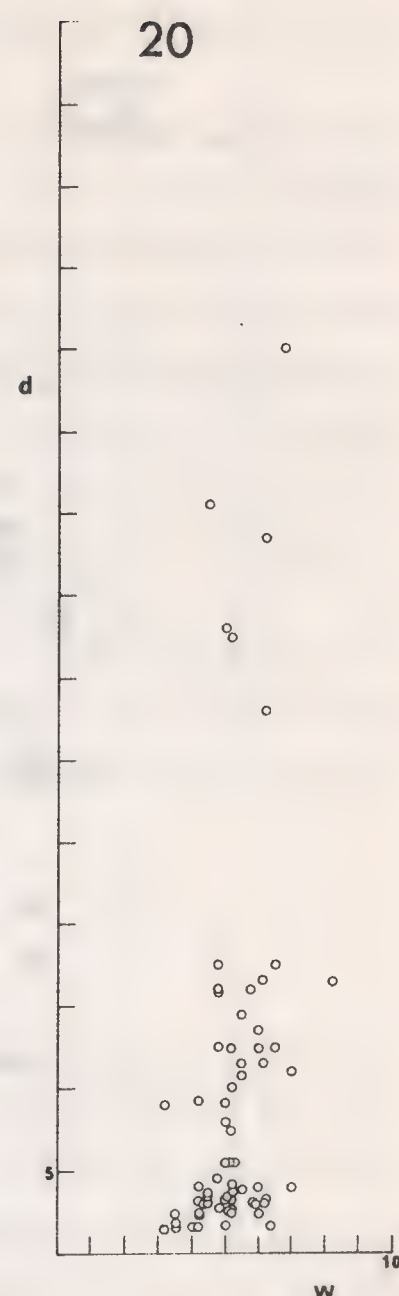
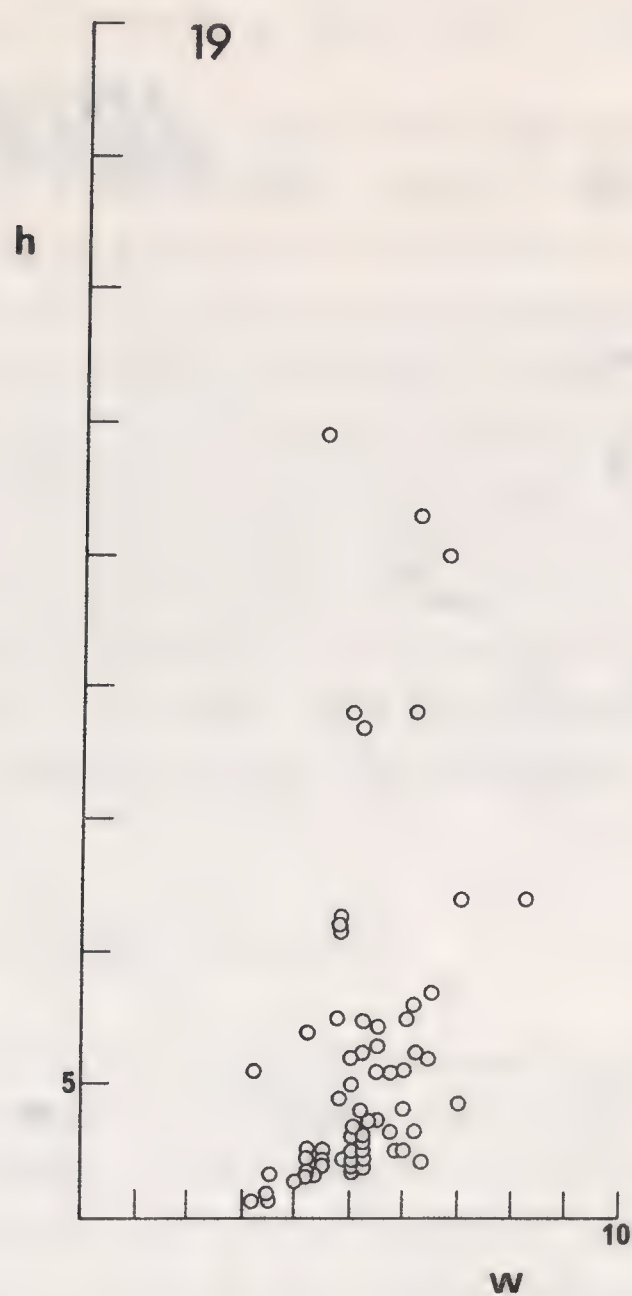
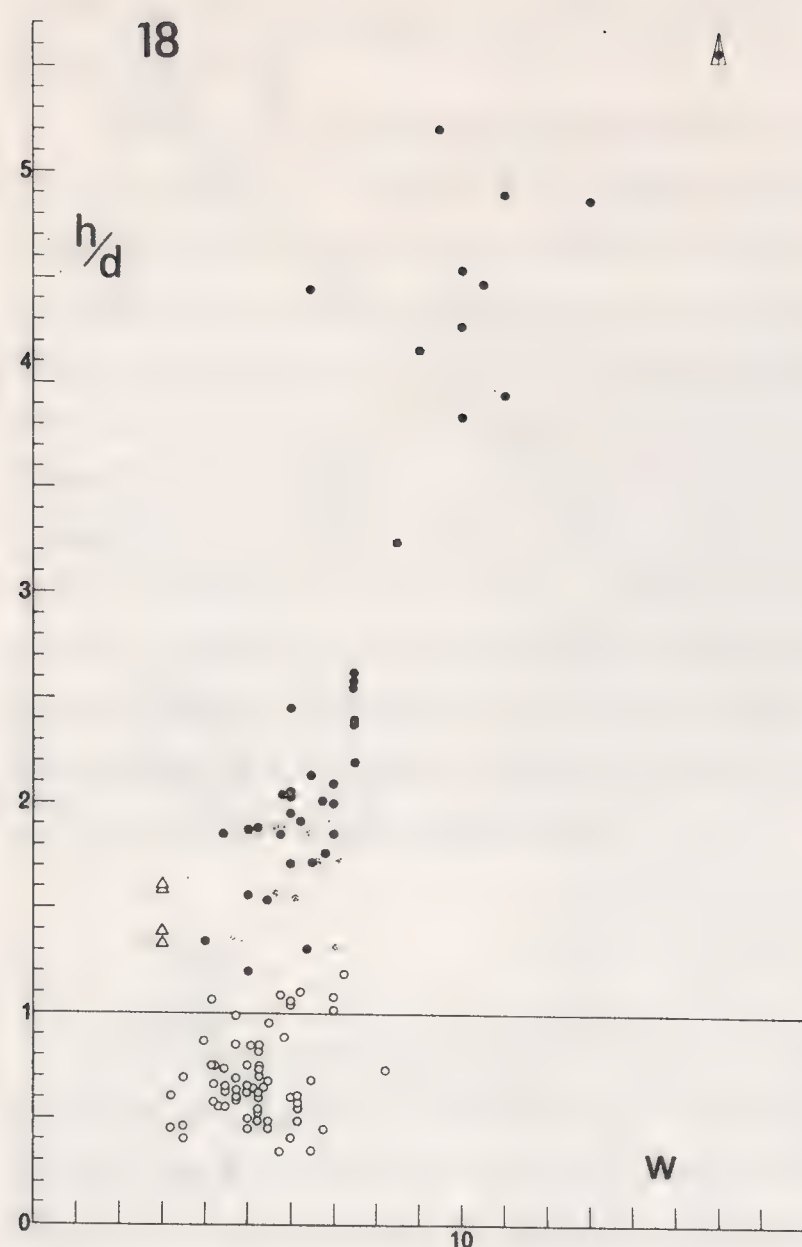


Fig. 18. Javanese terrestrial pulmonate fauna; scatter diagram for  $h/d$  (ordinate) against  $w$  (abscissa). Symbols as in figs. 1 and 7. The triangular pointer indicates the direction of a species off the diagram,  $h/d = 6.68$ ,  $w = 16.5$ . Fig. 19. Javanese fauna, L group;  $h$  (ordinate) against  $w$  (abscissa). Fig. 20. Javanese fauna, L group;  $d$  (ordinate) against  $w$  (abscissa). Fig. 21. Javanese fauna, U group;  $h$  (ordinate) against  $w$  (abscissa). Fig. 22. Javanese fauna, U group;  $d$  (ordinate) against  $w$  (abscissa).



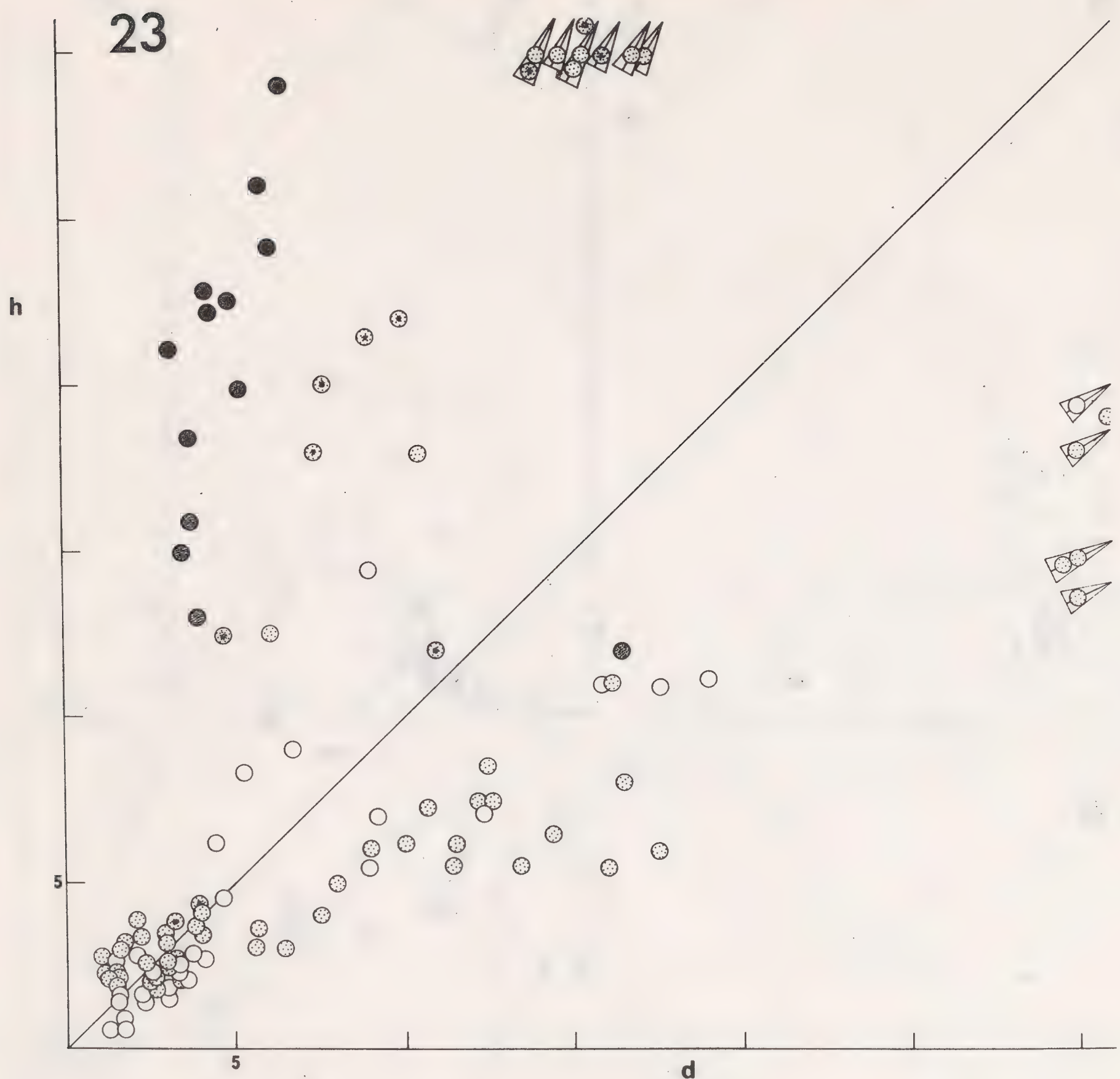


Fig. 23. Javanese fauna; scatter diagram for  $h$  (ordinate) against  $d$  (abscissa), symbolized for whorl number. Symbols as in figs. 6, 12, and 17; pointers carry appropriate symbols for, and point in the direction of, a few species too large to go into the diagram; they agree well with the pattern shown.

apposed, circulation might be hindered by both friction and capillary forces. A study of the viscosity of the body fluids might be useful here.

The close association of high whorl number with very elongate shells ( $h/d$  more than 3) might perhaps be expected on constructional grounds. The possession of a large number of whorls means in effect that inside the envelope formed by all those parts of the shell visible exteriorly are a large number of cross-partitions acting as a sort of continuous strut to strengthen the whole shell – the illustration of a sectioned shell of *Terebra* given by D'Arcy Thompson (1942, p. 818) makes the point clear. What is unexpected is the considerable range of shapes, from  $h/d$  values of about 0.4 to about 2.5 within which there is very little association of  $h/d$  and  $w$ , and for which resistance to deforming forces is presumably adequate even though the number of internal supporting walls seen in a sectioned shell varies greatly. An investigation of the properties of molluscan shell as a constructional material is required to take this matter



further. The purpose of the present paper is only to point out the phenomena that need investigating.

Lastly, the marked difference in regression of  $h/d$  upon  $w$  for the upper scatter between the faunas (figs. 1, 7 and 18) needs comment. In the North American fauna as a whole, whorl number increases more rapidly with increase in  $h/d$  than in the French or Javanese faunas. Two possibilities can be suggested; either the shells are on the whole thinner in the North American fauna, and more whorl walls are required as cross-struts to support the shell against deformation and consequent breakage, or predator-pressure is (or was in the near past) stronger in North America, so that even with normally thick shells, more internal support is required. This latter possibility implies that there are North American predators not strong enough to crunch up adult shells but able to demolish individuals with fewer whorls or thinner shells than usual. The former suggests a fauna living largely in non-calcareous habitats and forced to redesign the shell for extreme economy in calcium carbonate. Are bush- and tree-dwelling snails affected by a shortage of calcium carbonate even in limestone areas? No data exist at present for further discussion of such questions.

## ACKNOWLEDGEMENTS

I am greatly indebted to Dr. G. Alan Solem for raising the question, permission to work on the Field Museum molluscan collections, reading the typescript and great hospitality. Dr. G. M. Davis kindly checked my determinations of whorl number in the selected helicostyline and read the typescript, as did Dr. R. Robertson. I am further indebted to Professor J. D. Currey, Dr. R. A. D. Cameron, Mr. D. P. T. Burke and Mr. R. H. Cowie for criticizing an earlier draft of this paper.

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## OBITUARY

John Wilfrid Jackson

(1880–1978)

Dr. John Wilfrid Jackson died on 16th November, 1978, in his 99th year. His first publications, more than 20 notes and short papers on land and freshwater Mollusca of Lancashire and Derbyshire, appeared in the *Journal of Conchology* from 1901 to 1907. In the latter year he was appointed to the staff of the Manchester Museum, where he was in charge of the geological collections, but the trend of his early interests remained throughout his long and distinguished career. When he finally retired to Buxton, in 1945, his department was augmented with many cabinets of Recent Mollusca, a fair proportion of which he had named and labelled himself. Added to these were the cabinets of the Conchological Society and its library. Yet all were packed tight enough to allow room for work in the confines of part of the Museum basement, as his then young successor can testify. The situation, and Jackson's adaptation to it, reflects something of the repleteness, breadth and energy of his professional life. J. Wilfrid Jackson, as he preferred to sign himself, was an all round naturalist in the best traditions of the late Nineteenth Century. To conchology he added expert knowledge of local natural history, cave Mammalia, archaeology and Carboniferous palaeontology. But for three quarters of the present century he succeeded in keeping to the forefront of each increasingly specialized discipline.

J. W. Jackson was born in Scarborough, but soon moved with his family to Manchester, where he was educated. He entered first the cotton, then the woollen trade and continued his education by evening class work at the Manchester School of Technology. By 1901 he was a keen collector and student of land and freshwater Mollusca, working in both the Manchester region and in Derbyshire. His earliest published work consists of reports of rambles of the Conchological Society and the finds he made himself. He was a regular exhibitor at meetings for many years after this date and made important contributions to the *Journal*, notably his 'Bibliography of non-marine Mollusca of Lancashire' published in four parts (*J. Conch., Lond.* 12, 1907–9). Other work was published in the *Naturalist* and the *Lancashire Naturalist* of this period and his reports began to cover progressively wider areas of the north of England.

The Manchester Museum greatly extended Jackson's interests. Learning from W. Boyd Dawkins, he made many reports on cave Mammalia and on archaeological finds. The collections themselves, rich in Carboniferous material also provided him with much scope for work, notably on Mollusca. However as with his first approach to conchology, Jackson laboured extensively and successfully in the field, notably in the Carboniferous limestone areas of Derbyshire and the Namurian of the Edale district. The latter work was particularly rewarding, enabling him to recognize the presence of the lower Namurian Chronozones in the Edale Shales. When the then Geological Survey (Institute of Geological Sciences) revised the Manchester and adjacent sheets in the early 1930s Jackson did much to help with systematic work on Namurian marine bivalves. Indeed he was one of the few palaeontologists of his time to apply wide knowledge of living groups to the interpretation of fossil faunas. This knowledge he extended to Recent brachiopods (*Trans R. Soc. Edinb.*, 48 (1913)), publishing further work on South African Recent Brachiopoda in 1952.

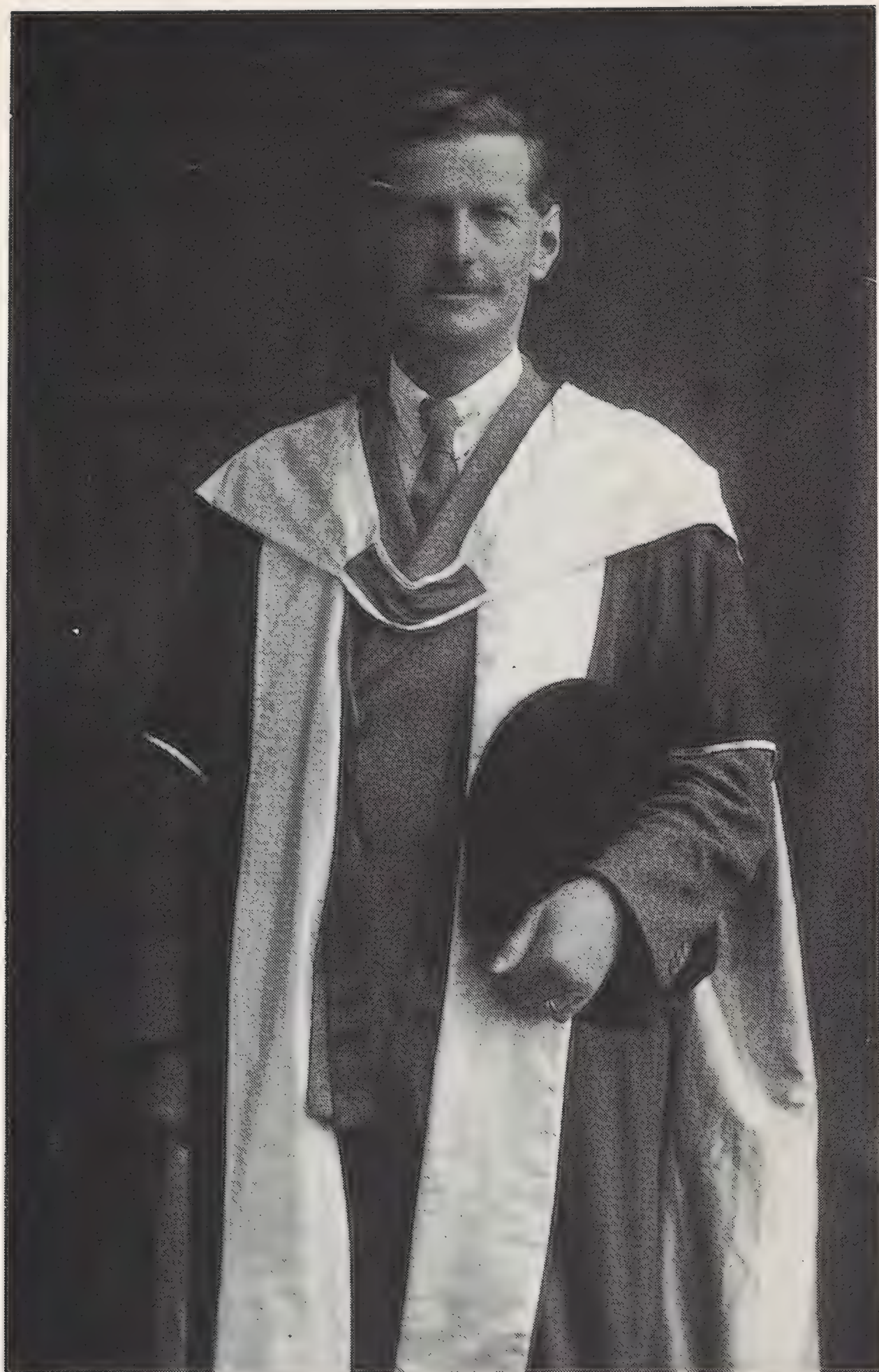
In spite of the much widened range of his studies from 1907 onward, Jackson continued his work with the Conchological Society, regularly publishing short papers and notes, particularly on freshwater gastropods, until 1924 when he was President. His Address at this time, 'The distribution of *Margaritana margaritifera* in the British Isles' utilized palaeontological evidence as well as extensive private records. The Society also owes to him the account of its founding and early history (*J. Conch., Lond.* 18, p. 65). In the succeeding years his conchological interests continued and amongst his occasional publications in the *Journal* were notes on *Corbicula fluminalis* (1932) and *Pisidia* (1941).

Jackson received the Degree of D.Sc in 1929 and was much honoured by conchologists, archaeologists and especially geologists, receiving the award of the Murchison Fund in 1934, and the Silver Medal of Liverpool Geological Society in 1949. However despite all his scientific achievement, which involved the publication of over 150 papers, Dr. Jackson will be remembered most, by the people who know him, as a source of inspiration, particularly to the young. He was a fine leader in the field and a gifted, inspiring teacher of several generations of students of the University Extra-Mural Department and the Workers Educational Association. Moreover he carried on with his lectures to the age of ninety.

Alicia his wife died in 1952. His only son Robert died in 1977. To his daughter, also Alicia, who looked after him to the end, his many friends, colleagues and students owe a great deal.

R.M.C.E.





*J. Wilfrid Jackson,*  

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1929.







## REVIEWS

Monographs of Marine Mollusca. Edited by R. Tucker Abbott. No. 1. The Family Cerithiidae in the Indo-Pacific. Part 1. 'The Genera *Rhinoclavis*, *Pseudovertagus* and *Clavocerithium*' by Richard S. Houbbrick. Loose-leaf; 130 pp. Pub. by American Malacologists, Inc. U.S.\$15.00

To those who are acquainted with '*Indo-Pacific Mollusca*', now sadly no longer to be published, this monograph will be received as a pleasant surprise. It was obviously prepared for that publication, is of the same high standard as previous monographs published under its umbrella, and is in the same format.

The opening twenty-eight pages contain an Introduction, Materials and methods, Acknowledgements, History of generic nomenclature, Biology, Hybridization, Anatomy, List of recognized taxa, Choice of criteria, Geographic distribution and phylogeny, Doubtful species of rhinoclavid snails (some fifty species with remarks and synonymy for each) and lastly three and a half pages of a selected bibliography. The rest of the monograph divides the subfamily Cerithiinae into genera and subgenera, with details of the species, recent and fossil in each.

Recent species are dealt with under the headings 'Range', 'Depth range', 'Remarks', 'Habitat', 'Shell description', 'Animal description', 'Measurements', 'Synonymy', 'Nomenclature' and 'Records'. Photographs of the radula and a distribution map are given with each. Three colour plates are included as well as black-and-white photographs of shells within the text. Fossil species are dealt with under 'Range', 'Remarks', 'Description' and 'Synonymy', accompanied by a black-and-white photograph.

Very few U.K. collectors of the genera covered by this monograph (and there are few enough collectors of the family Cerithiidae anyway) will have specimens of more than a few of the Recent species covered. They will none the less find the monograph fascinating and satisfying. No doubt its publication will attract more collectors towards taking an interest in the family, and it is hoped, will encourage dealers and collectors in the field to offer more specimens to enable the collector at home to study them.

A monograph of this kind inevitably arouses interest in the family with which it deals, and those people who have the *Indo-Pacific Mollusca* paper on the Cassidae (Part I), published in August 1968, are still waiting for Part II as promised; similarly with the family Mitridae. One appreciates the amount of work and research which goes into such monographs, but one still looks forward to the complete work, and hopes the further work on the Cerithiidae will not be too far away.

Finally a comment on the production. It is unfortunate that in a work of such a high standard, the proof reading should not have been perfect. In the 'Key to Living Species of *Rhinoclavis* s.s.' on page 31, there is a line missing: '6(5) . . . . . 7', which should differentiate the species *sinensis* and *diadema* from *articulata*. However that such an error should stand out is only a tribute to an otherwise excellent publication.

A. P. H. OLIVER

*Marine Mollusca of East Scotland*. By David W. McKay and Shelagh M. Smith. Published by the Royal Scottish Museum, December 1979. (Review copies published by the Nature Conservancy Council, 1979.) 185 pages, plus eight introductory and four full-page maps. 364 species maps, printed on A4 paper.

The production of this atlas of the Marine Mollusca of East Scotland is a very brave attempt to tackle a most difficult and thorny aspect of biological mapping. The sea unlike the land, does not have regular and easily recognizable landmarks. It is important, therefore, when recording off-shore, to give very precise co-ordinates if the records are to be of any real value when producing distribution maps.

Much of the equipment needed for this purpose is fairly sophisticated, and not always readily available to small boat operators. It is important, therefore, that an easily recognizable system for mapping marine organisms should be used. In this respect it is understandable that most of the off-shore workers prefer to give their co-ordinates on a latitude/longitude basis, a system which is well-established, easily used, and available on most maps covering both sea and shore. It is this system which has been favoured by the authors of this atlas.

Point mapping on a latitude/longitude basis is used by some of the marine mapping schemes at present in progress, but a more common form of mapping is that used by the land-based recording groups, viz. the now almost ubiquitous National Grid, 10 km sq. system. One of the problems of the latitude/longitude point mapping system is that excessive concentrations of data tend to build up around centres of activity. To avoid this, the authors have grouped their data on a grid basis, using an area 1/25th of an I.C.E.S. statistical rectangle, 6' of lat.  $\times$  12' of long. an area approximately equivalent to an 11 km square (in the area of Eastern Scotland covered by this survey).

This is ideal for the purposes of the present publication, but could, however, lead to much confusion when comparing maps published in the different styles.



The area covered by the present publication has boundaries drawn arbitrarily at 55° 30' N. to 58° 30' N, and eastward from the coast to 04° 22' W of the Greenwich Meridian. Within this area, 414 species of marine Mollusca have been recorded, although 39 are asterisked as being 'with all probability, invalid records'. Of the 414 species included in the atlas, only 364 are mapped. The maps are of only limited use with regard to the distribution and range of our native marine Mollusca, owing to the lack of data nationally.

The authors must have spent a great deal of time and effort in the gathering of information for the atlas, but even then it can only be considered very provisional. If the data available are examined, one finds that over 30% of the species listed have no recent, i.e. post-1950, records and a further 10% have only one recently recorded locality. The coastal areas are, on the whole, very well covered but, as might be expected, the sea has a less than 50% cover. Of the 400 area units, well over 100 have not been sampled at all. This cover, however, is probably better than could be expected nationally.

One of the main problems with this type of atlas, based on a limited survey area, is that at the present time no comparisons can be made with similar areas elsewhere. The publication of this atlas must have caused the authors a great deal of heart-searching and many weeks of discussion before the present format was adopted. On the whole, however, I think both authors can be congratulated for persevering and producing what will undoubtedly be a very useful work of reference for the future.

A. NORRIS.

*Tropical Pacific Marine Shells*. By Walter O. Cernohorsky. 352 pp., 68 plates, (4 coloured). Pacific Publications, 1978. Price £17.50.

'Tropical Pacific Marine Shells' is a continuation and the third volume of 'Marine Shells of the Pacific', volumes I and II of which were published in 1967 and 1972, respectively. Collectors who use the first two volumes will be delighted at the publication of a third volume which is in the same format as vol. II.

This volume contains in its first 26 pages, a list of contents, general remarks on shell-collecting, arranging a collection and identification; seven pages of 'Molluscan Classification' giving the classes, subclasses, orders, superfamilies and families in the phylum, and a figure showing the terminology of a gastropod shell. There follow 163 pages of descriptions of some 600 species, including 16 pages on bivalves. There are then 68 plates of photographs, four of which are in colour. The latter cover 35 species of cones and one miter. Two pages on 'General References', three on 'Regional Molluscan Bibliography' (supplementary to the titles listed in Vol. II), a Glossary, a table of measures and an index, complete the total of 352 pages.

Vol. I covered only a few of the popular families and generally the more common members of them. Vol. II made some additions to Vol. I and covered the more common species of the families not included in Vol. I. Vol. III, as would be expected generally deals with the uncommon to rare species not included in its predecessors. In addition taxonomic changes affecting some species in the first two vols. are given, and in some families a list of corrections incorporating nomenclatural changes has been included.

It is interesting that thirteen pages are devoted to the Nassariidae, covering some forty odd species. The Mitridae and Costellariidae (replacing the later name Vexillidae), as one would expect from Cernohorsky who is perhaps the leading authority on these families, take up another thirteen pages each. The Conidae are covered in twenty-five pages, the majority of species rare, the rest mostly moderately rare to uncommon. The Turridae also take fifteen pages. The other twenty-five families of gastropods and twelve of bivalves are each covered in a few pages.

Like Vol. II, the descriptions are clear and concise. Habitat, depth (tidal or subtidal), as well as range and main synonyms are given. The photographs, both colour and black-and-white, are excellent. Dates of names, sadly so often omitted by modern authors, are given.

It is a pity that on page 65, *Chicoreus palmarosae* Lamarck, 1822 is given as a synonym for *C. rosarius* (Perry, 1811). In fact, as Dr. Emily Vokes has pointed out in the *Annals of the Natal Museum* 23, p. 386, the ICZN reached a decision in 1974 on secondary homonymy which at last settled this problem, and the name given by Lamarck and in current use for so long, continues to apply. This, however, is a small point to quibble over in an excellent book.

To any serious collector or student of tropical Indo-Pacific shells, especially gastropods, this book will be most welcome. It is a worthy successor to Volume II.

A. P. H. OLIVER



## INSTRUCTIONS TO AUTHORS

Authors of papers submitted for publication in the *Journal of Conchology* are urged to pay careful attention to the following notes. Any author who has difficulty in complying with these requests, or has queries concerning manuscripts, should consult the Hon. Editor **before** submitting a manuscript.

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2. **Two** copies of all text and illustrations should be submitted. (A few years ago the entire copy for one issue of the *Journal* was lost in a mail robbery!). Authors are strongly recommended to retain a further copy for proof correction.

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4. Originals of text-figures should be  $1\frac{1}{2}$ –2 times the final size but should not exceed 25 by 36 cm. They should be drawn in Indian ink on clean ground, numbers consecutively, and referred to in the text as “Fig. 1”, etc. Authors are strongly urged to construct text-figures so as to make full use of the page width and to submit a copy reduced to final (published) size wherever possible. Lettering should be legible and not less than 1 mm high after reduction.

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7. All papers referred to in the text (including synonymy lists) should be listed alphabetically by author's surnames at the end of the text under “References”. For books give author's name, initials, date, full title, pages, plates and place of publication.

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BROWN, P. and STRATTON, G. B. (Editors). 1965. *World list of scientific periodicals published in the years 1900–1960* (4th Ed.) 3 vols. London.

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WOODWARD, F. R. 1965. Monograph of the British Lower Tertiary Unionidae, with descriptions of three new species. *J. Conch., Lond.* **25**: 316–330, pls. 22–27.

GOULD, S. J. 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail. *P. (Poecilozonites)* in Bermuda. *Bull. Mus. comp. Zool. Harv.* **138**: 407–532, 5 pls.

8. Authors may obtain copies of all papers at cost price if ordered from the printers, via the Hon. Editor, when the galley proofs are returned.



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# COCHLICOPA LUBRICA AND OTHER ALIEN TESTACEOUS LAND SNAILS IN SOUTH AFRICA

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Department of Systematics and Evolutionary Biology of the University,  
c/o Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands

(Read before the Society, 18 February, 1980)

*Abstract:* *Cochlicopa lubrica* (Müller) is added to the list of alien land mollusc species in southern Africa (breeding colony in Northcliff, Johannesburg).

Throughout the world alien molluscs are a threat to man and his agricultural activities and also to the native malacofauna. Vastly increased transport possibilities have led to the naturalization of many foreign species of land gastropods, particularly in countries such as South Africa and Australia. Unfortunately the lists of alien taxa are continually increasing without ever a single report of foreign snails disappearing for good. Southern Africa has already more than its share of naturalized foreign terrestrial pulmonates (Van Bruggen, 1964, 1967), so that it is with considerable regret that we have to add yet another species.

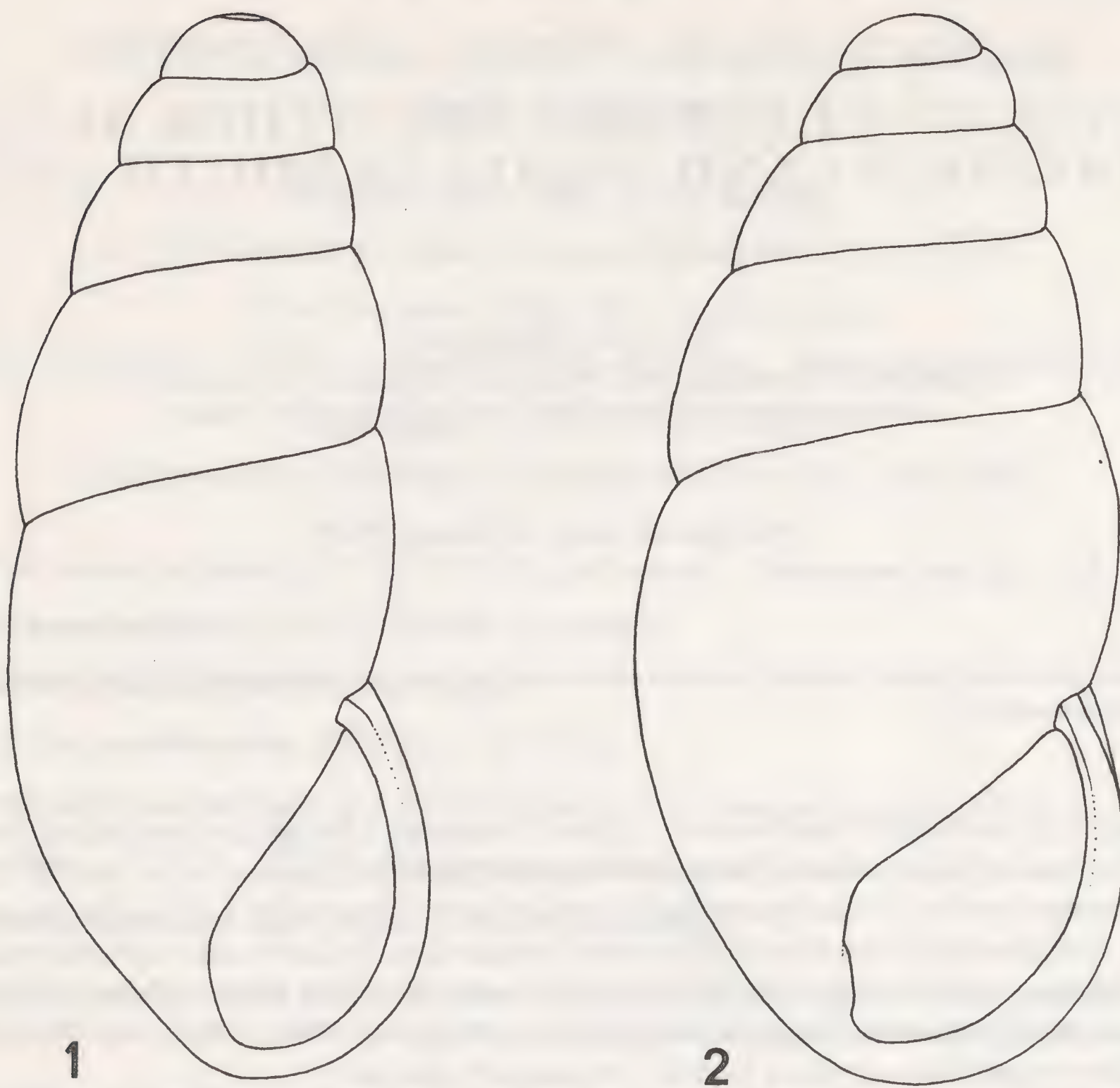
Abbreviations used are l/d for the ratio length/major diameter of shells (all l/d values have been calculated from micrometer readings) and RMNH for Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.

In 1978 the indefatigable mollusc collector Dr. H. E. van Hoepen, a Johannesburg neurologist/psychiatrist, discovered a thriving colony of *Cochlicopa lubrica* (Müller) on his property, 188 Acacia Road, in Northcliff, a northwestern suburb of the sprawling city of Johannesburg (Transvaal), in a shed on a whitewashed wall and outside under a heavy 40 gallon drum on slasto paving (flagstones).

*Cochlicopa lubrica*, a species new to the South African list, has a very wide distribution, aptly summarized by Kerney and Cameron (1979) as being Holarctic. In addition it has been reported from various other countries outside its natural range as an alien (St. Helena island, cf. Crowley and Pain, 1977; Australia, cf. Burch, 1976; New Zealand, cf. Zilch and Jaeckel, 1962; Venezuela, cf. Zilch and Jaeckel, 1962). Some of these data are from a period when all forms were lumped together as *C. lubrica* and material should be reviewed in the light of the new taxonomic conception. The present author has seen some Australian material in the Western Australian Museum (Perth) in 1979 and this is certainly due for revision.

The closely allied species *C. lubricella* (Porro) has been reported from South Africa, i.e. from Grahamstown in the Eastern Cape Province (Van Bruggen, 1967). This is also a Holarctic species, albeit less widely ranging than *C. lubrica*. Recently *C. lubricella* has also appeared in the Transvaal. Mr. W. D. Haacke of the Transvaal Museum (Pretoria) submitted a sample of this species received from Mrs. Esson, who found the snails in Bryanston in May 1977 'dead in huge concentrations on a slasto paving in her garden as well as in the pumphouse' (Haacke, *in litt.* 4.V.1977; material in Natal Museum, Pietermaritzburg, duplicates in RMNH). [The mollusc collections of the Transvaal Museum, Pretoria, have been transferred to the Natal Museum,





Figs. 1–2. Outlines of *Cochlicopa* shells from South Africa, 1. *C. lubricella* (Porro), Grahamstown, 5.2 mm long (RMNH); 2. *C. lubrica* (Müll.), Northcliff, 5.2 mm long (RMNH).

Pietermaritzburg.] Bryanston is a northern suburb of Johannesburg, situated NE of Northcliff. This material may be summarized as follows: 4.7–5.1 × 2.0–2.1 mm, 1/d 2.35–2.50. The Grahamstown material (Van Bruggen, 1967: 502) appears to be somewhat larger: 5.0–5.6 × 1.9–2.1 mm, 1/d 2.38–2.84.

The two species are difficult to distinguish; recent sources describing the differences well are Gittenberger, Backhuys and Ripken (1970; pp. 45–46) and Kerney and Cameron (1979; p. 62). The main differences in the shells are the comparatively broad apex in *C. lubricella* and the mean major diameter (2.1 mm), and the comparatively much narrower apex in *C. lubrica* and the larger mean major diameter (2.6 mm) in the shell of this species. The shell of *C. lubricella* (4.5–6.8 mm long) is also somewhat smaller than that of *C. lubrica* (5.0–7.5 mm long); moreover, the shell of *C. lubricella* is consistently more slender than that of *C. lubrica* (see below).

Measurements of South African adult shell material are shown in Table 1. The table amply shows that the material (Figs. 1–2) so far recorded from South Africa clearly represents two different taxa. There is a slight overlap in the length of the shell, but both major diameter and 1/d are completely separate.

The first record of *C. lubricella* in South Africa, Grahamstown, may perhaps be explained by the proximity of the local Botanic Gardens. The Bryanston locality is a garden in a residential suburb; it is possible that the species has been imported with garden plants from Europe (perhaps even the United Kingdom). As regards the Northcliff locality of *C. lubrica*, Dr. Van Hoepen has



# TESTACEOUS LAND SNAILS IN SOUTH AFRICA

TABLE 1

Comparison of measurements of adult shells of *Cochlicopa lubricella* (Porro) and *C. lubrica* (Müller) from South Africa. B = Bryanston, G = Grahamstown, Bryanston material in RMNH, Grahamstown material after Van Bruggen, 1967. All *C. lubrica* are from Northcliff.

|         | <i>C. lubricella</i>                | <i>C. lubrica</i>                   |
|---------|-------------------------------------|-------------------------------------|
|         | 4.7 × 2.0 mm, l/d 2.38 B            | 5.0 × 2.4 mm, l/d 2.05              |
|         | 4.9 × 2.0 mm, l/d 2.50 B            | 5.1 × 2.4 mm, l/d 2.13              |
|         | 4.9 × 2.0 mm, l/d 2.50 B            | 5.1 × 2.5 mm, l/d 2.05              |
|         | 4.9 × 2.1 mm, l/d 2.35 B            | 5.2 × 2.4 mm, l/d 2.21              |
|         | 5.0 × 2.0 mm, l/d 2.50 G            | 5.2 × 2.6 mm, l/d 2.00              |
|         | 5.0 × 2.1 mm, l/d 2.41 B            | 5.3 × 2.5 mm, l/d 2.12              |
|         | 5.0 × 2.1 mm, l/d 2.41 B            | 5.4 × 2.4 mm, l/d 2.20              |
|         | 5.0 × 2.1 mm, l/d 2.38 G            | 5.4 × 2.5 mm, l/d 2.15              |
|         | 5.1 × 1.9 mm, l/d 2.68 G            | 5.4 × 2.5 mm, l/d 2.15              |
|         | 5.1 × 2.1 mm, l/d 2.47 B            | 5.4 × 2.5 mm, l/d 2.15              |
|         | 5.2 × 2.0 mm, l/d 2.60 G            | 5.5 × 2.5 mm, l/d 2.20              |
|         | 5.3 × 1.9 mm, l/d 2.79 G            | 5.5 × 2.6 mm, l/d 2.09              |
|         | 5.3 × 2.1 mm, l/d 2.52 G            | 5.7 × 2.6 mm, l/d 2.19              |
|         | 5.4 × 1.9 mm, l/d 2.84 G            |                                     |
|         | 5.6 × 2.1 mm, l/d 2.67 G            |                                     |
| range   | 4.7–5.6 × 1.9–2.1 mm, l/d 2.35–2.81 | 5.0–5.7 × 2.4–2.6 mm, l/d 2.00–2.21 |
| mean    | 5.1 × 2.0 mm, l/d 2.59              | 5.3 × 2.5 mm, l/d 2.10              |
| average | 5.1 × 2.0 mm, l/d 2.53              | 5.3 × 2.5 mm, l/d 2.13              |

kindly tried to trace the source of importation. Dr. Van Hoepen has lived on his plot since 1948 and much of his garden still has remains of the original vegetation with *Acacia karroo* as the dominant tree species. The plot is situated on the northern slopes of a row of hills termed Aasvoëlkop. The few plants recently added to the garden were locally obtained from locally propagated stock. The neighbour's garden does not harbour *Cochlicopa* snails. Nevertheless, the most likely source of these gastropods is the nursery from where the plants were obtained. Dr. Van Hoepen (*in litt.* 7.X.1979) has suggested that drums with fertilizer, swimming pool chemicals, building material, etc. may be the source of these imported snails. Many of the Northcliff specimens of *C. lubrica* had themselves attached to the bottom of one of these drums. At times, these may be left standing outside for long periods before being shipped to their respective destinations overseas. Drums transported from Europe may well have carried *C. lubrica* to South Africa. It is certainly possible that *C. lubrica* has been in South Africa for quite some time; its small size and cryptic colour may have contributed to the fact that it has only been discovered in 1978.

It is surprising that both *Cochlicopa* species seem to thrive in the generally dry climate of South Africa. The habitat of *C. lubrica* is described by Kerney and Cameron (1979; p. 62) as 'Catholic: moderately damp places of all kinds; marshes, grasslands, woods.' *C. lubricella* occurs 'characteristically in drier places than *C. lubrica* (limestone grassland, calcareous sand dunes, screes) but the two species are often associated.' Obviously the South African garden climate seems to suit the species well enough; we may forecast little danger of these snails becoming established in wilder places in South Africa.

It is convenient to add the following new records of alien testaceous pulmonate species of land molluscs for South Africa (early data summarized by Van Bruggen, 1964, 1967).

*Vallonia pulchella* (Müller): Lambton (Germiston, Transvaal), D. W. Aiken garden, leg. R. Aiken, 2 May 1971 (RMNH). So far known from Pretoria, Pietermaritzburg, Kingwilliamstown, Grahamstown, Port Elizabeth, Somerset East, Cape Town and Cape Peninsula, and Melkbosstrand.

*Oxychilus (Oxychilus) cellarius* (Müller): *ibidem*, leg. R. Aiken, April 1972 (RMNH). So far known from Bulawayo, Kimberley, Somerset East, Somerset West, Stellenbosch, Cape Town and Cape Peninsula.



*Oxychilus (Ortizius) alliarius* (Miller): *ibidem*, leg I. Aiken, May 1972 (RMNH); Bryanston (Johannesburg), leg. Mrs. Esson, May 1977, with *C. lubricella* (Natal Museum, RMNH). So far only known from Grahamstown, Cape Town and Cape Peninsula.

*Cochlicella barbara* (Linnaeus): Bloemfontein, in garden, leg. Dr. J. A. Pringle, 2 May 1970 (Natal Museum, RMNH). So far known from scattered coastal localities from Cape Town and the Cape Peninsula to the Natal south coast. This is only the second alien species for Bloemfontein, the third alien species for the Orange Free State, and, most interesting, an inland instead of a coastal locality.

*Helix (Cornu) aspersa* Müller: Nelspruit town lands (Transvaal), leg. P. S. Visser (RMNH). Very widely distributed in the Transvaal, Natal, and Cape Province; in the Cape Province populations have assumed pest proportions in the wine-growing districts.

Tribute is paid to the collecting activities of Dr. Van Hoepen, who also kindly read through the manuscript of this paper; other material was contributed by Dr. J. A. Pringle and Messrs. D. W. Aiken and C. C. Appleton. Dr. E. Gittenberger (RMNH) has rendered assistance with certain identifications.

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# A TECHNIQUE FOR THE ASSESSMENT OF PREDATION BY BIRDS AND MAMMALS ON THE SLUG *DEROCERAS RETICULATUM* (MÜLLER) (PULMONATA: LIMACIDAE)

A. SOUTH

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(Read before the Society, 18 February, 1980)

*Abstract:* Jaw width and body weight show a significant correlation for each of three slugs examined—*Deroceras reticulatum*, *Arion hortensis* and *Milax budapestensis*. The jaws of slugs and snails resist digestion in the gut of bird and mammal predators. Under certain conditions, the jaw of *D. reticulatum* can be recognized and the size of slugs eaten may be estimated from jaws recovered from the gut of a predator, using a regression line. This technique has been used to study predation of slugs by starlings, hedgehogs, shrews and moles. Since slugs are agricultural pests, the technique may be useful for assessing the effect of vertebrate predation on slug populations.

Little is known about the effect of predators on slug numbers. The available information, mainly relating to bird predation, tends to be contradictory (Runham and Hunter, 1970). Digestion of slugs is rapid, particularly in birds, and the only structures which resist digestion are the jaw, radula and, very occasionally, fragments of the internal shell. It is difficult to relate these remains to the size of slugs ingested (Pernetta, 1976). During a study of the ecology of the slug *Deroceras reticulatum* (Müller) on permanent pasture in Northumberland (South, 1965), examination of bird gut contents showed that, although jaws were generally recovered intact, radulae were often fragmented and could not be identified. It was also found that jaws from individuals of *D. reticulatum*, with a body weight greater than 50 mg, could be recognized and an estimate made of the body weight of the slug eaten. This technique has also been applied to slug jaws taken from gut contents and faeces of several small mammals.

## PREPARATION OF JAWS

Jaws were dissected from the buccal mass of freshly-killed slugs and snails and mounted in polyvinyl-lactophenol. If the jaw was difficult to remove, it was freed from tissue by macerating the buccal mass in 10% potassium hydroxide solution. The jaw width was measured to within 15  $\mu$ m, using an eyepiece graticule. Jaw length was not used since accurate determination was complicated by the variable extent of chitinization of the posterior margin of the jaw and the variable beak development of some species, particularly *Milax budapestensis* (Hazay).



## IDENTIFICATION OF JAWS

Waldén (1976) lists 117 species of British terrestrial slugs and snails, excluding greenhouse and other alien species. Of these, three (*Testacella* spp.) have no jaw, six (*Pomatias elegans* (Müller) and the Succineidae) have distinctive jaws (Taylor, 1894–1921) and about fifty species either rarely attain a body weight, excluding shell, of 40 mg or, have jaws less than 800  $\mu\text{m}$  wide. The remaining species may be divided into two groups on the basis of jaw form. The latter is either crescent shaped and markedly ribbed (odontognathous; Plate 7, Fig. 1) or relatively smooth and usually with a median anterior projection or beak (oxygnathous; Plate 7, Figs. 2 and 3). The former group comprises the Helicidae and Arionidae while the latter group includes the Limacidae, Milacidae and several zonitid and vitrinid snails.

*Oxygnathous jaws.* The width of zonitid jaws, with the exception of that of *Oxychilus draparnaudi* (Beck), rarely exceeds 1 mm and this is confirmed in volume 3 of Taylor (1894–1921). Zonitid jaws examined showed little or no pigment and the beak was often poorly developed. These features enabled them to be distinguished from the more heavily pigmented limacid and milacid jaws which showed, in addition, a darkening near the attached margin and a well developed beak. The larger jaw of *O. draparnaudi* could be distinguished from those of smaller slugs by these features. Taylor (1894–1921) confirmed that the beak of this species is only slightly developed but also described it as being pigmented. The jaw of the common vitrinid snail, *Vitrina pellucida* (Müller), has a prominent beak but is less than 1 mm in width. Runham and Thornton (1967) examined the ventral surface (i.e. the surface exposed to the buccal cavity) of the jaw of *D. reticulatum* using a scanning electron microscope. They found numerous poorly defined fine groovings approximately parallel to one another but at an angle of  $20^\circ$  to the longitudinal axis of the jaw. These were absent where the centre of the jaw was produced as a beak (Plate 8, Fig. 2). Examination of 144 jaws of *D. reticulatum* (between 57 and 706 mg body weight) in the present investigation, using optical microscopy, showed agreement with these observations. The oblique fine groovings were visible on dry jaws, using reflected light, and, less clearly, on jaws mounted in polyvinyl-lactophenol. No grooves were seen in the region of the beak although, as Runham and Thornton observed, this appeared very rough especially on dry jaws. The ventral surface of *Milax budapestensis* jaws showed, in addition to the poorly defined oblique groovings, deep distinct grooves covering the centre of the jaw and running parallel to the longitudinal axis of the jaw (Plate 8, Fig. 1). Although absent from the jaw of *D. reticulatum*, similar deep grooves were observed on the jaws of *Deroceras caruanae* (Pollonera), *Deroceras laeve* (Müller), *Milax sowerbyi* (Ferussac), *Milax gagates* (Draparnaud), *Limax maximus* Linnaeus, *Limax cinereoniger* Wolf, *Limax flavus* Linnaeus and *Limax marginatus* Müller. The grooves of *Limax* tended to be finer than those of *Milax* and might, with further investigation, provide a means of distinguishing between jaws of these genera. The use of these grooves for the identification of *D. reticulatum* jaws was tested on a mixed sample of 40 jaws from this species (66–645 mg body weight) and *M. budapestensis* (127–1051 mg), when only two jaws were incorrectly identified.

*Odontognathous jaws.* Limited observations suggest that these jaws may be grouped according to the form of the ribs. Jaws of *Cepaea* spp. and *Helix* spp. have few (2–8) narrow, prominent ribs. The jaws of several other helicids and arionids examined had more, broader and less prominent ribs. Taylor (1894–1921) suggested, however, that the number of ribs may be modified by diet (vol. 1, p. 255).

Specific identifications have been made of *D. reticulatum* jaws greater than 800  $\mu\text{m}$ , in width, recovered from the gut contents of birds. This has been helped by a knowledge of the distribution of slugs and snails in the vicinity of the study area and of the feeding range of the predators. Many slugs and snails are restricted in their geographical distribution (Kerney, 1976) and even common species are often restricted to certain habitats (Boycott, 1934; Evans,



PLATE 7 SLUG JAWS

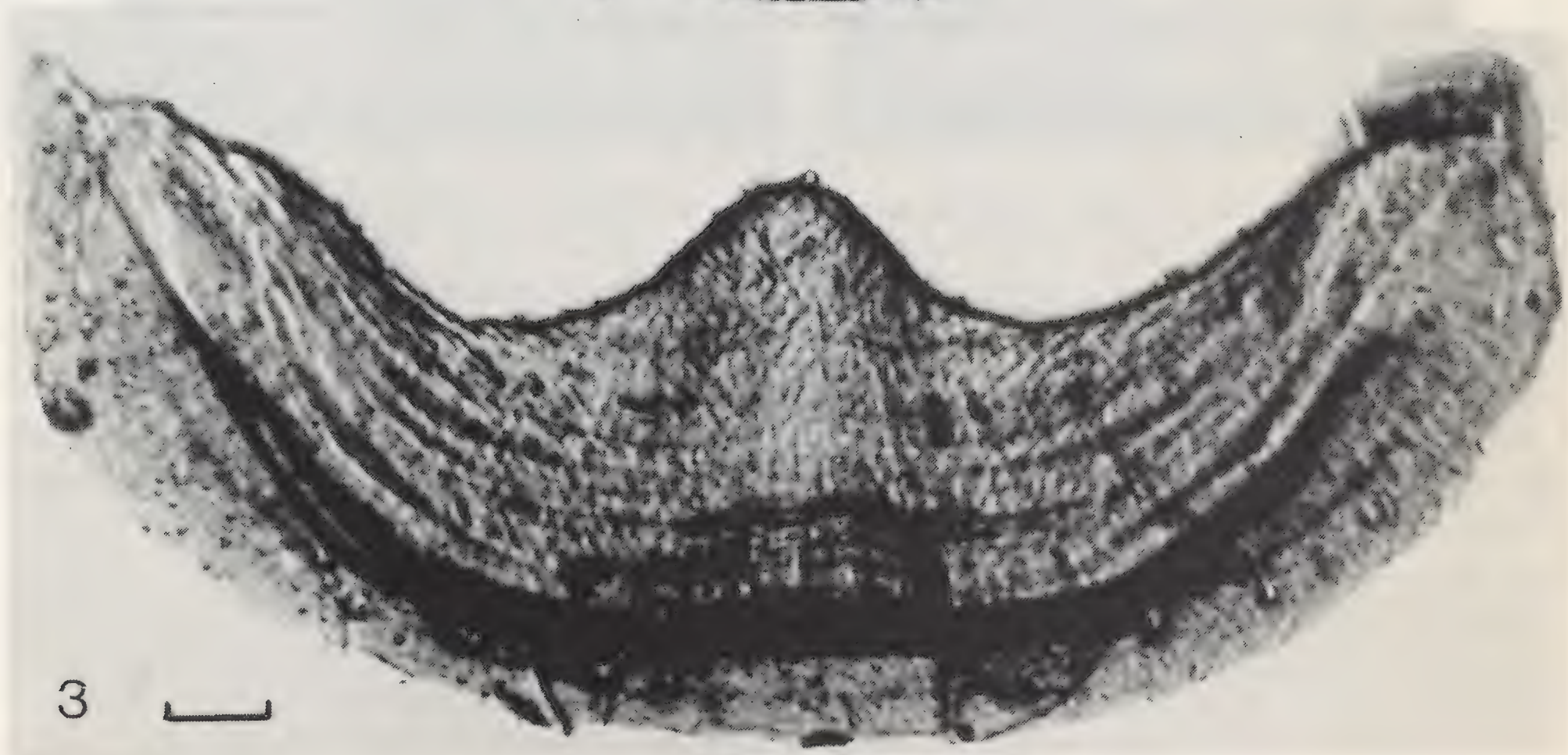


PLATE 7 Ventral views of slug jaws (1) *Arion circumscriptus* (odontognathous), (2) *Milax budapestensis* (oxygnathous), (3) *Deroceras reticulatum* (oxygnathous). Slugs from Paddock Wood, Kent. Scale: 100  $\mu$ m.



PLATE 8 SLUG JAWS

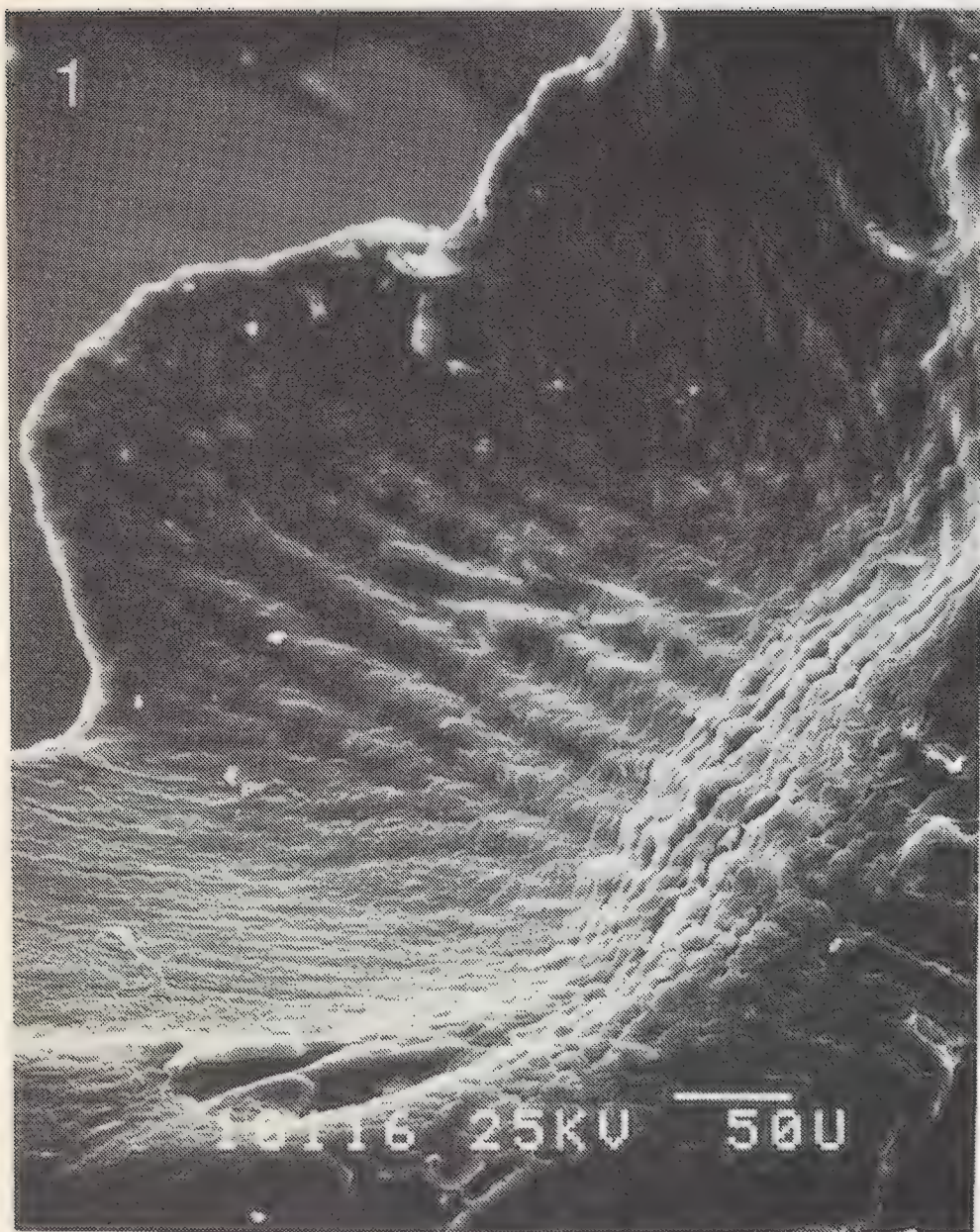


PLATE 8 Scanning electron micrographs of ventral aspect of beak of slug jaws: (1) *Milax budapestensis* (Nafferton Farm, Northumberland) (2) *Deroceras reticulatum* (Paddock Wood, Kent). Scale: 50  $\mu$ m.



## ASSESSMENT OF PREDATION BY BIRDS AND MAMMALS

1972). Smaller oxygnathous jaws, corresponding to slugs of less than 50 mg body weight, are poorly pigmented and may be confused with those of *Oxychilus* spp. or *Vitrina* spp. However, jaws of very young oxygnathous slugs (less than 20 mg body weight) have a double beak, evidence of the bilateral origin of the jaw (Quick, 1960), and it is often possible to distinguish these from jaws of smaller species of snail with jaw widths less than 400  $\mu\text{m}$ .

### RELATIONSHIP BETWEEN JAW WIDTH AND BODY WEIGHT

A total of 114 *D. reticulatum* jaws was examined from six samples taken from Frindsbury, Kent (TQ 744698) (15 individuals), Paddock Wood, Kent (TQ 665453) (22 and 30 individuals), Orierton Field Centre, Pembrokeshire (SR 955992) (20), Nafferton Farm, Northumberland (NZ 065657) (8) and Monks Wood N.N.R., Huntingdonshire (TL 200800) (19). Slugs varied from 57 to 706 mg body weight. There was a significant overall correlation between body weight and jaw width ( $r_{114} = 0.835$ ;  $P < 0.001$ ). The regression coefficient for jaw width on body weight for the 114 slugs was  $1.595 \pm 0.099 \mu\text{m}$  per mg body weight. Comparison of individual samples showed no significant difference between the slopes of positions of regression lines for individual samples. A regression line fitted to the data was used to estimate body weights of slugs eaten by predators, using the widths of jaws recovered from gut contents and faeces of the predators examined below.

Significant correlations were also found between jaw width and body weight for *Arion hortensis* Ferussac (2 samples) and *Milax budapestensis* (1 sample), correlation coefficients ranging from 0.804 to 0.885 (all significant at  $P < 0.001$ ). The regression coefficients for jaw width on body weight for the combined *A. hortensis* data and for *M. budapestensis* data were 1.723 and 1.161  $\mu\text{m}$  per mg body weight respectively.

TABLE 1

Comparison of % frequency distribution of weights of *D. reticulatum* estimated from jaws recovered from gut contents of starlings with weights from routine samples

| Estimated slug weights (mg)       | 0-50    | 51-100  | 101-150 | 151-200 | 201-250 | 251-300  |
|-----------------------------------|---------|---------|---------|---------|---------|----------|
| % frequency—routine samples       | 54.1    | 16.2    | 13.5    | 8.1     | 2.7     | —        |
| % frequency—starling gut contents | 12.4    | 11.2    | 6.7     | 15.7    | 5.6     | 4.5      |
| Estimated slug weights (mg)       | 301-350 | 351-400 | 401-450 | 451-500 | 501-550 | over 551 |
| % frequency—routine samples       | —       | 5.4     | —       | —       | —       | —        |
| % frequency—starling gut contents | 18.0    | 5.6     | 6.7     | 6.7     | —       | 6.7      |

### ASSESSMENT OF BIRD PREDATION

A sample of thirteen starlings (*Sturnus vulgaris* Linnaeus) was taken after the birds had been observed feeding in the study area (permanent pasture) at Nafferton Farm, Northumberland, for several hours in February. The contents of the gut, anterior to the duodenum, were gently washed through a 125  $\mu\text{m}$  aperture sieve and then examined for slug remains under a low-power microscope. There were no snail shell fragments but a total of 89 oxygnathous and four odontognathous jaws was recovered from the gut contents. The latter jaws measured between 813 and 1438  $\mu\text{m}$  in width and were probably from individuals of either *Arion intermedius* Normand or *Arion circumscriptus* Johnston agg. weighing between 50 and 400 mg, since these were the only arionid slugs present in the study area at the time and no larger snails were present. Other slug remains recovered included a portion of radula and several fragments of limacid



shells, probably from *D. reticulatum*. The oxygnathous jaws were identified as those of *D. reticulatum*, the number of jaws recovered from each starling ranging from two to twenty-nine. The remaining gut contents consisted mainly of dipterous larvae (especially Tipulidae and Bibionidae) and other insect remains, earthworm cocoons and varying amounts of vegetable material. Table 1 compares the percentage frequency of slug weights, estimated from *D. reticulatum* jaws using the regression line given above, with the frequency distribution of weights of thirty-seven *D. reticulatum* taken in routine samples from the study area at that time.

#### ASSESSMENT OF MAMMAL PREDATION

Jaws and other remains were recovered by washing a faecal pellet (fresh weight 1.14 g) of a hedgehog (*Erinaceus europaeus* Linnaeus) taken from a garden at Paddock Wood, Kent, during October. Fifteen jaws were recovered comprising eleven *D. reticulatum*, three other large oxygnathous and one odontognathous jaws. Several small fragments of radulae were also found. The estimated body weights of *D. reticulatum* ranged from 160–396 mg together with three less than 50 mg. The oxygnathous jaws were probably from *M. budapestensis* of 600–700 mg body weight, since these were the only other oxygnathous slugs or snails of this size present. The odontognathous jaw, 1275  $\mu\text{m}$  wide was probably from an arionid slug. Examination of other faecal samples from hedgehogs at other times of the year confirmed that slugs are frequently taken by hedgehogs except when weather conditions are unfavourable to slug activity.

The entire gut contents of fourteen common shrews (*Sorex araneus* Linnaeus) and three pygmy shrews (*Sorex minutus* Linnaeus), taken from mixed deciduous woodland at Monks Wood N.N.R., in May, were examined for slug and snail remains. All the shrews had consumed appreciable amounts of food and five jaws were recovered, including one from the gut of a pygmy shrew. One jaw was recognizable as that of a small individual of *D. reticulatum* (90–100 mg body weight) and a second oxygnathous jaw (760  $\mu\text{m}$  wide) was probably that of a zonitid snail. The remaining three odontognathous jaws ranged from 600–1000  $\mu\text{m}$  in width and had about ten broad, low ribs. The recognizable remains of a small *Arion circumscriptus* Johnston agg. were also found with one of the jaws in the gut of a pygmy shrew. It seems probable that the odontognathous jaw also belonged to this species which was common in the woodland. Two similar jaws and a portion of radula were the only mollusc remains recovered from the gut contents of ten moles (*Talpa europaea* Linnaeus) taken from the same habitat.

#### DISCUSSION

Slug jaws have not been used previously to study the effect of vertebrate predation on slug populations although a similar use has been made of cephalopod beaks recovered from the stomachs of whales and other predators (Clarke, 1962). The present study has shown that jaws may be recovered entire from the gut contents of birds and from faeces and gut contents of some mammals. Oxygnathous jaws of *D. reticulatum* can be identified with sufficient accuracy to enable them to be used to estimate the original size of slugs from a regression of jaw width on body weight. Some limited identification is possible for other oxygnathous and odontognathous jaws exceeding 1000  $\mu\text{m}$  in width and this is helped by a knowledge of the slugs and snails present in the feeding area of the predator. The identification of smaller (less than 1000  $\mu\text{m}$ ) jaws is less reliable for species other than *D. reticulatum* because of the much larger number of species involved.

The results of the examination of gut contents of starlings feeding on permanent pasture suggest that these birds readily take slugs and that they tend to select larger individuals. Their



method of feeding, by probing the turf and upper layers of the soil, means that surface-living slugs, such as *D. reticulatum*, are readily available to starlings. Slugs have been recorded in the diet of starlings by Collinge (1921) and Schermer (1958) although Dunnett (1956) did not consider them as a significant source of food in his study of the autumn and winter food of starlings. There are many recorded instances of hedgehogs feeding on slugs, e.g. Brockie (1959) found that they were eaten frequently and Dimelow (1963) showed that hedgehogs in captivity readily accept slugs although tending to reject some *Arion* spp. These observations agree with the results obtained from the examination of slug jaws in hedgehog faeces. The small number (five) of jaws recovered from the gut of fourteen common and three pygmy shrews suggests that slugs are not important components of the diet of these insectivores. This is supported by the conclusions of Pernetta (1976). Similarly, results of the present study suggest that slugs are not frequently taken by moles and a similar proportion was found by Macdougall (1942). Raw (1966) found small numbers of slugs in moles' stomachs and concluded that they occur less frequently than might be expected from their abundance in the soil fauna.

Since the conclusions obtained from the examination of slug jaws recovered from predators agree with those recorded in the literature, it appears that this technique might be applied successfully in the assessment of the effects of predation on *D. reticulatum* populations. One disadvantage of this method is that the rate at which jaws pass through the gut is not known and this makes it difficult to estimate absolute numbers of slugs eaten. It is possible, however, to decide whether a predator has been feeding on slugs and to obtain some indication of the size range of individuals eaten. It also allows comparisons to be made of the diets of different predators.

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## REVIEW

*Living Seashells. Molluscs of the English Channel and Atlantic Coasts.* By P. Bouchet, F. Danrigal and C. Huyghens. Translated and edited by B. E. Picton. 144 pp., many coloured plates. Blandford Press, Poole. 1979. Price £4.95

This book was originally published, in 1978, as *Coquillage des Côtes atlantique et de la Manche*, and the title must be understood as referring to the French Atlantic coast. After an introduction to molluscan classes, it discusses in turn the main coastal habitats and the ecology and biology of some of their molluscs. There follows a series of photographs of molluscs, usually in natural settings; finally ten plates illustrate the shells of some 140 species.

I am not sure for whom this book is intended; the publisher's blurb claims it 'should prove to be a standard identification work for marine biologist, beachcomber, diver or tourist', while the authors more modestly declare that its aim is 'to familiarize people with some of the most attractive of these molluscs in their living state'. The former it is not, while the latter it does admirably. The marine biologist will hardly agree that he is 'bound to ask what the little soft sacks are which send out a jet of water when they are pressed', or that Aeolids are 'very cunning animals'. Nudibranchs are mentioned several times before we are told that they are 'shell-less molluscs', 'dorids' and 'Rissoids' are not explained, and I wonder what the beachcomber will make of the abbreviation 'spp.' There are several other blemishes: for example the flat winkle is twice called *L. obtusata* and twice *L. littoralis* while indexed as the latter; the genus *Triphora* is called *Triforis* although one of the authors argues elsewhere (Bouchet and Guillemot, 1978) 'that the European Triforidae are *Triphora* s.l., not *Triforis*'. and while the picture of the animal is captioned *Triforis perversa*, it is indexed as *Triforis adversa* which it cannot be, and it seems identical to the *Triphora similior* illustrated in the above-mentioned paper; the section on beaches implies that *Turritella*, *Dentalium* and *Caecum* live in sand *intertidally* which I would regard as unusual at least on this side of the Channel; *Abra alba* is said to form 'vast populations on the mudflats', which I would regard as more applicable to *A. tenuis* and in fact the animals depicted although somewhat obscured by sand, could be of the latter species, particularly since they show the rather characteristic staining near the shell margin; the northern limit of *Assiminea littorina* is given as the Bay of St. Malo which ignores the records from the south coast of England; the shell of *Alvania crassa* is wrongly named '*Alvania semistriata*'.

But these are details. The many photographs of the living animals are superb, and among the best I have seen. The delightful *Tricolia* waving all its tentacles from the front of the book sets the standard for a host of masterpieces, as for example *Antiopella* on *Bugala*, the series of bivalve siphons, *Odostomia scalaris* inserting its proboscis into a mussel, the cuttlefish peering from the sand. How useful to illustrate the spawn of various species; a comprehensive guide to mollusc spawn by the authors would be welcomed by many conchologists. Some animals depicted have rarely been photographed—*Galeomma turtoni* crawling like a gastropod, *Balcis* on a sea cucumber, *Alvania lactea*. The enthusiasm of the authors for the living animals probably shows most in the 'pair' of *Bittium reticulatum* and *B. simplex* illustrating well how different they are and how easily distinguished. Bernard Picton's translation and editing is lively and enjoyable particularly in the many references to nudibranchs.

The colour plates of shells are not so successful and for the most part they duplicate figures easily available elsewhere. But the pictures of live animals are valuable and a pleasure to examine; they justify the book and its price.

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D. R. SEAWARD



## MONACHA OBSTRUCTA (PULMONATA: HELICIDAE) FROM SAUDI ARABIA, A NEW RECORD

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(Read before the Society, 19 April 1980)

*Abstract:* The first record of *Monacha obstructa* from Saudi Arabia is reported, and its geographical distribution described. Shells of this species were found buried deep in the sand dunes in remote situations. Human agency may have been responsible for their presence.

Land and freshwater molluscs have been reported from various parts of the Arabian Peninsula, specifically Saudi Arabia, Yemen and Oman, by Blanford (1875), Joussaume (1890), Melvill and Ponsonby (1895), Ancey (1906), Pallary (1928), Connolly (1941), Wright (1963) and Smythe and Gallagher (1977). *Monacha obstructa* (Férussac, 1824), which belongs to the family Helicidae, has not been recorded from Arabia by the above workers. Tristram (1884) recorded *Helix obstructa* from the Phoenician plain (western Palestine), Germain (1921) found it at Damascus (Syria), Beirut and Tyre (Lebanon), around the Dead Sea, Jerusalem, Kemlach and Haifa (Palestine), and Biggs (1959) collected *M. obstructa* near the bank of the river Karun, which flows through Iraq and Iran (Fig. 1). These workers thus reported *M. obstructa* from the northern Middle East.

In the present note the author records the presence of *M. obstructa* from the southern Middle East (Saudi Arabia) and describes its distribution. The shell was identified by comparing it with *Helix obstructa* collected by Mr. J. W. Jackson from Ramleh, Egypt and deposited in the Merseyside County Museum, Liverpool, England (Registration No. 1942, 22). Specimens of *M. syriaca* (Ehrenberg) and *M. olivieri* (Férussac) are present in the museum.

### DISCOVERY

During the academic periods 1977/78 and 1978/79 in Saudi Arabia I searched carefully for the shells of land snails and collected them whenever out in oases and nearby localities. Of the various groups of invertebrates represented near Al-Hair (Fig. 1), *M. obstructa* was the most abundant in number of individuals. Samples of 400 shells were obtained in which live ones were in the minority. No attempt was made to study the live ones. Shells were brought to the laboratory, washed, dried and preserved for further study. Samples were collected at midday in January from Al-Hufuf and in February from Al-Hair (Fig. 1) when the average temperature was 22°C.





Fig. 1. Distribution of *Monacha obstructa* in the northern Middle East. Locations are shown by + signs.

#### DESCRIPTION

Shell medium sized, thin walled, translucent, depressed above and convex below with slightly elevated spire. Suture deep, mouth rounded, umbilicus open and deep, columellar lip slightly reflected, surface smooth, glossy with faint transverse striation. Colour greyish-white to yellowish-white with a paler peripheral band. There are differences in shell-characters in the closely related species of *Monacha* commonly found in the northern Middle East. These are *Monacha syriaca*, *M. olivieri* and *M. obstructa*. Apart from other conchological characters they can fairly quickly be identified by looking at the umbilicus. *M. syriaca* has no umbilicus. There is a narrow umbilicus in *M. olivieri* and an open and deep one in *M. obstructa*. Height: 5–5.5 mm; Breadth: 10–11 mm; Number of whorls:  $4\frac{1}{2}$ –5.



## HABITAT AND DISTRIBUTION

Live *M. obstructa* were collected from damp, shaded, grassy and well-vegetated regions at Al-Hufuf (Lat. 25°, 20'N, Long. 49°, 34'E) in the eastern province of Saudi Arabia and at Al-Hair (Lat. 24°, 22'N, Long. 45°, 50'E) in the central province (Fig. 1). The distance between these localities is about 500 km. I have been on collecting trips many times in the oases during my stay in Saudi Arabia. It is conceivable that living shells may pass from one oasis to another by human agency especially when the camels are the only means of transport by Beduins (nomadic people) over this arid land. It is customary to break the journey, spread the tent and relax wherever there is water and vegetation before proceeding on towards the destination. Land snails can become established near the permanent pools and surrounding vegetation. It seems unlikely that dispersal of land snails has taken place by the winds. Hot and strong winds, sand storms and movement of sand during summer may lead to the desiccation of the snails, if they happened to be blown away. I found shells in remote situations deep in the sand dunes where the vegetation generally failed, due to aridity. I do not think that sufficient importance has been attached in the past to the possibility of such means of dispersal over vast regions in Saudi Arabia. At present rapid changes in using the underground water of cave-lakes and springs for agriculture, regulating the temporary streams after occasional rains and stabilizing the sand dunes, have led to the presence of more vegetational patches in Saudi Arabia. Further sampling from these patches in the western and northern provinces may reveal the presence of the species in question.

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## PRECOCIOUS BREEDING OF *THEBA PISANA* (MÜLLER) PULMONATA: HELICIDAE)

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(Read before the Society, 17 May, 1980)

*Abstract:* *Theba pisana* (Müller) can breed successfully when only approximately half-grown, that is, with a maximum shell diameter of less than 10 mm.

During the course of a programme of research on the helcid land snail *Theba pisana* (Müller) a sample of snails was taken from Tenby, South Wales (National Grid reference SN 132001) on 16 November 1979. The animals were kept dry in plastic lunch-boxes lined with paper until 28 November when a subsample of thirty snails was removed and put in a box lined with 4 cm of sterilized soil and kept at room temperature. The maximum shell diameters of the snails in this subsample ranged from 7.1 mm to 9.6 mm. On 30 November a clutch of eggs was seen about 0.5 cm below the soil surface and against the clear side of the box. After a few days embryos could be seen in some of the eggs.

Observations on the Tenby colony of *T. pisana* have been continuing for three years. It has become clear that it usually takes two years for the snails to grow to full adult size (up to about 20 mm maximum shell diameter) and that the snails mentioned above belong to a one-year-old cohort and are approximately half-grown. Viable sperm has also been observed in the hermaphrodite duct of snails of about 10 mm shell diameter (for a description of this technique see Bett, 1960).

These observations show that *T. pisana* is capable of breeding at an unexpectedly small size and early age. Though a similar behaviour has been observed in some non-helcid families (e.g. Mordan, 1978), *T. pisana* is in this respect most unlike other helcids such as *Cepaea nemoralis* (L.), which only become reproductively mature when fully grown and with a thickened lip at the aperture of the shell (Lang, 1904). (I have, however, seen *Helix aspersa* Müller mating when almost fully grown but without a thickened lip.) Since snails may be capable of sperm storage from a number of matings, extreme caution must be exercised when setting up breeding experiments, so that sufficiently immature, and therefore virgin, animals are used. This is now obvious for *T. pisana* but may be equally applicable to other helcid snails.

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# REPRODUCTION AND GROWTH IN *ANOMIA* *EPHIPPIUM* (L.) (BIVALVIA: ANOMIIDAE) IN STRANGFORD LOUGH, NORTHERN IRELAND

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(Read before the Society, 17 May, 1980)

*Abstract:* The annual reproductive cycle of *Anomia ephippium* (L.) in Strangford Lough, N. Ireland was investigated from histological preparations of the gonad. Development proceeded rapidly during late spring until by June most individuals were fully ripe. Spawning occurred over the summer months (June–August) after which the reproductive follicles gradually regressed and the population entered a resting or spent phase. Changes in gross shell morphology occurred with increased body size. Shells became progressively more ovoid in shape with proportionately smaller byssal embayments in the lower valve. Differences in the relative rates of growth of the upper and lower shell valves are probably explicable in terms of their relative mechanical efficiencies. Shell growth was maximal during late spring and early summer.

Although superficially resembling true oysters (Ostreidae) saddle-oysters or jingle shells (Anomiidae) are in fact more closely related to byssally attached mussels. The name jingle shell derives from the Oriental habit of using these delicate shells as wind chimes. The anomiids are unique bivalves having the capacity for byssal cementation. They live permanently attached to the substratum by means of a calcified byssal plug which emerges through a prominent embayment in the lower (right) valve at right angles to the sagittal plane. The marked changes in symmetry of both the shell and the body that have occurred within this group are generally considered to be adaptations to their peculiar life style. Although they are monomyarian, the centrally placed posterior adductor muscle is here concerned primarily with shell movements which keep the mantle cavity free of pseudofaeces whilst the enlarged, subdivided byssus retractor muscle takes over much of the function of shell closure.

Apart from a few early publications (e.g. Gray, 1849; Morse, 1871; Sassi, 1905; Winckworth, 1922) surprisingly little attention has been devoted to the Family Anomiidae. *Anomia ephippium* (L.), the common saddle-oyster, is widely distributed, ranging from Iceland and the Faroes southwards to the Mediterranean and N. African coasts and into the S. Atlantic off the Falkland Islands (Tebble, 1966). It was first reported in Irish waters by Praeger (1899). It is exceedingly common in Lough Ine, S.W. Ireland (Renouf, 1931), and its distribution within the lough is tentatively attributed to predators such as crabs and starfish (Muntz, Ebling and Kitching, 1965; Kitching and Ebling, 1967). Seed and Roberts (1976) studied three distinct, but highly variable, anomiid populations in Strangford Lough, N. Ireland. Whereas *A. ephippium* was easily identified by virtue of its distinctive muscle scars, the separation of *Monia squama* (Gmelin) and *M. patelliformis* (L.) was exceedingly dubious, at least in terms of this particular shell characteristic.

Anomiid shells consist largely of a complex arrangement of calcite and aragonite (Taylor, Kennedy and Hall, 1969), though they are evidently toughened by the inclusion of a relatively



high proportion of organic material arranged in layers which can slide over one another when bent (Wainwright, 1969). Form and function within the Superfamily Anomiacea have recently been documented in considerable detail by Yonge (1977).

#### MATERIALS AND METHODS

All the material examined during this investigation was collected at extreme low water of spring tides from Greyabbey (Irish Grid 575675) a comparatively sheltered bay on the eastern shore of Strangford Lough, N. Ireland. Although Greyabbey Bay is predominantly sandy, extensive outcrops of bedrock and stones occur especially towards low water mark.

Throughout 1976 samples of *Anomia* (each containing 10–20 individuals) were collected at approximately monthly intervals. Reproductive tissue was removed immediately after collection, fixed in Bouin's fluid and stored in 70% alcohol. Small pieces of this tissue were subsequently embedded in paraffin wax (5–10 specimens could be accommodated in a single block) sectioned at 7  $\mu$ m and stained in Ehrlich's haematoxylin. From such sections each animal could be arbitrarily classified according to its degree of development and the density of gametes. Details of this classification are outlined below. The general reproductive condition of the *Anomia* population throughout the year was assessed by calculating a mean gonad index; this was obtained by multiplying the number of individuals in each stage by the numerical ranking of that stage and dividing the resulting value by the total number of individuals in that particular sample. A value of 0 would indicate that all individuals were completely spent, a value of 3 that the entire population was fully ripe. The index rises during periods of development and declines when spawning is in progress. From such histological preparations the cytological changes throughout the course of the annual cycle can be monitored in considerable detail.

(i) *The resting or spent gonad: Stage 0.*

Here the gonad has not yet become differentiated and there are no signs of sexual development.

(ii) *The developing gonad:*

Stage 1. This stage is characterized by the onset of gametogenesis. Although islands of germinal cells have begun to appear, no ripe gametes are yet visible.

Stage 2. A few ripe gametes have now appeared by this stage though the follicles, which are now fairly extensive, are still largely occupied by early stages of gametogenesis (spermatocytes, oocytes).

Stage 3. The swollen follicles are now densely packed with morphologically ripe gametes.

(iii) *The spawning gonad:*

Stage 2. During this stage there is a general reduction in the density of ripe gametes though large numbers are still retained within the follicles.

Stage 1. Spawning is now virtually complete and the follicles, containing only residual gametes, are starting to collapse and degenerate. Unspawned gametes are eventually phagocytized by amoebocytes.

*Anomia ephippium* in Strangford Lough has previously been shown to vary quite extensively in its overall shell morphology (Seed and Roberts, 1976). The contours of its shell closely follow those of the substratum to which the animal is attached (often small irregular cobbles or the shells of other molluscs). In view of such marked variations in overall shape only shells from flat rock surfaces, where growth was completely unrestrained, were used to investigate the pattern of relative growth. Shells were selected in order to provide an approximately equal representation of all the size classes present in the local *Anomia* population. Shell height (umbo-



# REPRODUCTION AND GROWTH IN *ANOMIA EPHIPIUM*

rim distance), length (anterior-posterior axis) and depth (the distance between the two valves) together with the maximum dimension of the byssal embayment (Fig. 1), were measured to the nearest 0.1 mm using sliding vernier calipers. After the tissues and any fouling organisms had been removed, the shells were dried and the upper and lower valves weighed separately to the nearest 0.1 g on a top loading balance.

Differential growth between the various size parameters measured was examined by testing each pair of size variables  $y$  and  $x$  for their fit to the allometric equation  $y = Ax^b$  where  $A$  and  $b$  are constants. In its logarithmic form this becomes

$$\log y = \log A + b \log x$$

so that if  $y$  and  $x$  are related allometrically they plot rectilinearly on logarithmic coordinates. The constants  $A$  and  $b$  were estimated by least squares regression.

A limited amount of data concerning the absolute rate of growth in shell height was obtained for the 1975 year class. Between April and September 1976 several small samples (10–21 individuals) of *Anomia* were collected from the shells of *Littorina littorea* (L.) and their mean shell height recorded. Details of this curious, yet relatively widespread association between saddle-oysters and periwinkles in Strangford Lough are documented elsewhere (Seed, 1977).

TABLE 1

Distribution of gonad stages in samples of *A. ephippium* from Strangford L. during 1976

| Month     | No. | Developing (%) |    |    | Spawning (%) |    | Spent (%) | Gonad index | °C <sup>1</sup> |
|-----------|-----|----------------|----|----|--------------|----|-----------|-------------|-----------------|
|           |     | 1              | 2  | 3  | 2            | 1  |           |             |                 |
| January   | 10  | 10             | 0  | 0  | 0            | 10 | 80        | 0.20        | 8.3             |
| March     | 19  | 84             | 0  | 0  | 0            | 0  | 16        | 0.84        | 7.1             |
| April     | 14  | 100            | 0  | 0  | 0            | 0  | 0         | 1.00        | 7.8             |
| May       | 20  | 80             | 20 | 0  | 0            | 0  | 0         | 1.20        | 9.0             |
| June      | 14  | 14             | 14 | 58 | 14           | 0  | 0         | 2.43        | 10.1            |
| August    | 18  | 0              | 0  | 0  | 11           | 22 | 67        | 0.44        | 13.5            |
| September | 19  | 0              | 0  | 0  | 0            | 32 | 68        | 0.32        | 13.3            |
| November  | 12  | 0              | 0  | 0  | 0            | 25 | 75        | 0.25        | 10.4            |
| December  | 13  | 3              | 0  | 0  | 0            | 8  | 84        | 0.15        | 9.2             |

<sup>1</sup> Average monthly surface sea temperatures in Strangford Narrows, Portaferry.

Temperatures for February, July and October were 7.2, 12.6 and 12.0°C respectively.

## RESULTS AND DISCUSSION

The annual reproductive cycle of the Greyabbey *Anomia* population throughout 1976 is summarized in Table 1 as percentages of the total population in each of the arbitrary stages, together with the gonad index for each month's sample. Since the samples were intentionally kept rather small (in the interests of conserving the local population) males and females are considered together. Whilst well over 100 saddle-oysters were sectioned and examined during this investigation no instances of simultaneous hermaphrodites were noted. Surface sea water temperatures in Strangford Lough over this period varied from a minimum of 7.0°C in March to 14.5°C in August.

During December and January virtually the entire Greyabbey population was in the resting condition though a few individuals had already started to redevelop. By March–April most animals showed some evidence of redevelopment as the germinal follicles started to reappear.



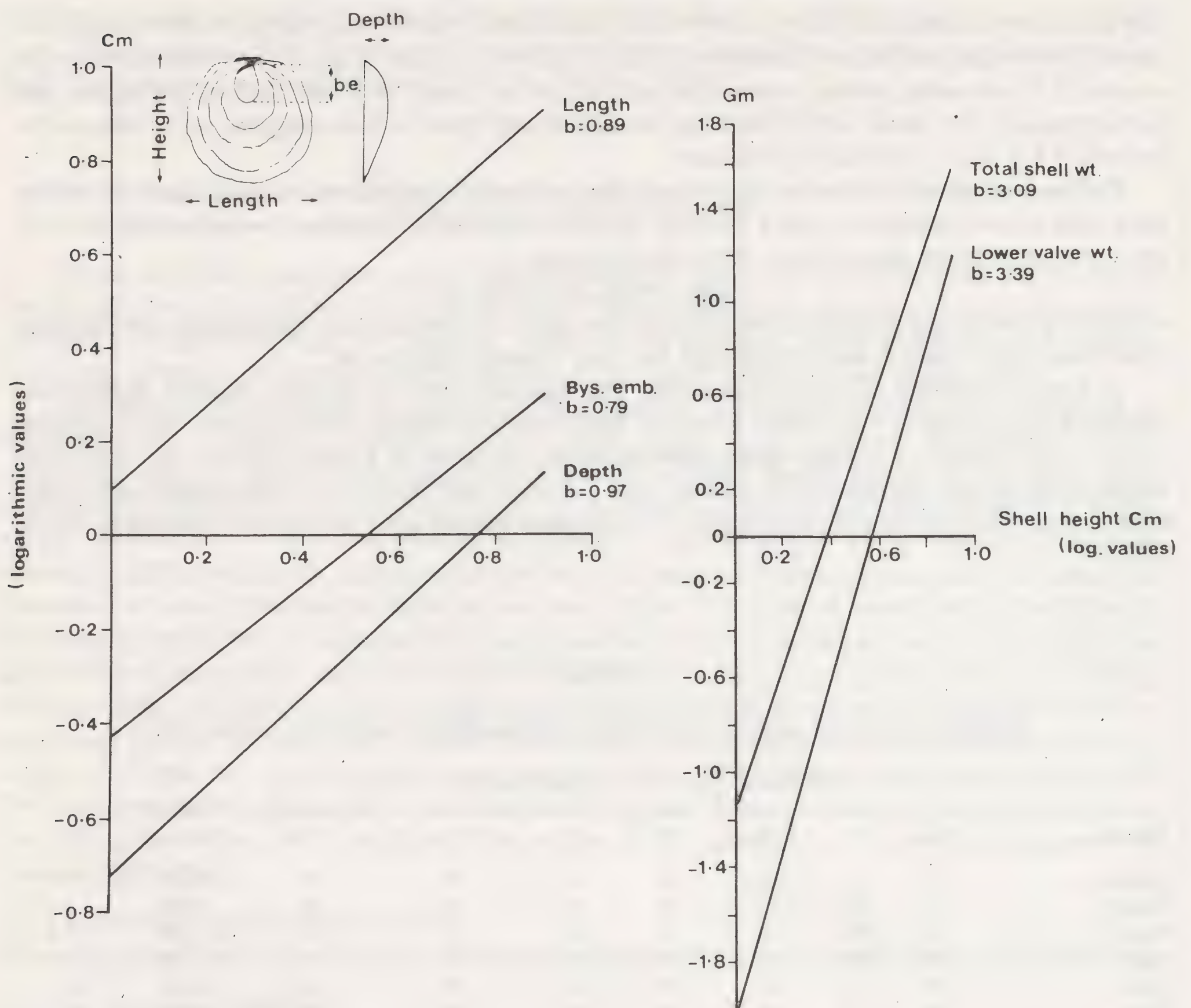


Fig. 1. Logarithmic regressions for length, byssal embayment, depth, total shell weight and lower valve weight as functions of shell height. The diagram (top left) illustrates the terminology of the anomiid shell. b. c. and bys. emb. byssal embayment.

TABLE 2

Coefficients of allometry for various combinations of size parameters in *A. ephippium*

| Dependent variable <sup>1</sup> | Independent variable <sup>2</sup> | Intercept <sup>3</sup> | Slope <sup>4</sup> | Coefficient of determination ( $r^2$ ) |
|---------------------------------|-----------------------------------|------------------------|--------------------|----------------------------------------|
| Shell length                    | Shell height                      | 1.27                   | 0.89*              | 0.94                                   |
| Shell depth                     | Shell height                      | 0.19                   | 0.97               | 0.80                                   |
| Byssal embayment                | Shell height                      | 0.37                   | 0.79*              | 0.88                                   |
| Total shell weight              | Shell height                      | 0.07                   | 3.09               | 0.93                                   |
| Lower valve weight              | Upper valve weight                | 0.27                   | 1.12*              | 0.86                                   |
| Upper valve weight              | Shell height                      | 0.05                   | 3.02               | 0.94                                   |
| Lower valve weight              | Shell height                      | 0.01                   | 3.39*              | 0.81                                   |

<sup>1</sup>The variable y and <sup>2</sup>the variable x in the equation  $y = Ax^b$ .

<sup>3</sup>The coefficient A and <sup>4</sup>the coefficient b in the equation  $y = Ax^b$ .

\* Values which depart significantly from isometry ( $P < 0.05$ ).



At this stage, however, it was still exceedingly difficult to establish the sex of any individual with any degree of certainty. Redevelopment proceeded rapidly throughout May so that by June most of the population was fully ripe. Spawning occurred during the summer months (the absence of a July sample is unfortunate) and by August most individuals were once again entering the resting or spent condition; this is especially noticeable by the pronounced fall in the mean gonad index from 2.43 in June to 0.44 in August. Although a few ripe gametes persisted in many individuals until well into the autumn and early winter months, these residual gametes were eventually phagocytized and by December the gonad index had reached its lowest value of the year. The breeding cycle of *A. ephippium* in Strangford Lough thus appears to be broadly similar to that previously reported for this species elsewhere in Ireland. Spawning in Lough Ine, S.W. Ireland was observed by Kilroy (1979) between July and October (though more especially during August and September). Larvae were present in the plankton throughout this period but they were particularly abundant in September. The normal developmental period in this anomiid seems to be approximately 20–30 days. Ebling, Kitching, Purchon and Bassindale (1948) also working at Lough Ine, found that most settlement occurred during September.

The intertidal *Anomia* population in Strangford Lough includes many unusually large individuals, some exceeding 9.0 cm in shell height. Those collected for this study varied from 2.1 to 7.7 cm in height, the largest specimens having a total shell weight of between 30–35 g.

When two size variables having the same units of measurement are related by a power function of the allometric type viz.

$$y = Ax^b$$

values of the exponent  $b$  greater than unity indicate that dimension  $y$  is increasing at a relatively faster rate than  $x$  (positive allometry). Values of  $b$  below unity indicate the reverse (negative allometry) whilst a value of unity for  $b$  is said to describe an isometric relationship in which the relative rates of growth for the two variables are identical thereby maintaining geometric similarity with increasing size. If, however, the dimensions of  $x$  are different from those of  $y$  then different criteria for isometry and allometry apply, e.g. if  $y$  is a weight (g) and  $x$  is a linear dimension such as height or length (cm) then  $b = 3$  will correspond to isometry.

Fig. 1 illustrates the relationships that exist between the various shell parameters and shell height when these are plotted on logarithmic coordinates. These data are summarized in Table 2 in terms of the coefficients  $b$  (slope) and  $A$  (intercept) of the allometric equation. Shell depth, total shell weight and the weight of the upper valve were more or less isometrically related to shell height. Length and the size of the byssal embayment, on the other hand, exhibit significantly negative allometric trends ( $b = 0.89$  and  $0.79$ , respectively) indicating that as the shell grows so it becomes more ovoid (i.e. the length/height ratio increases) with a proportionately smaller byssal embayment. These growth patterns imply that changes in overall shell morphology accompany the increase in body size. This is further evidenced by reference to Table 3 in which the changes in shell proportions are summarized. It must be remembered, however, that the *Anomia* shells used in this investigation were collected from flat surfaces where 'normal' growth was unrestrained. Many saddle-oysters settle and grow on irregular surfaces in such a way that their shells frequently closely follow the contours of the substrata to which they are attached. *Anomia* from small pebbles or the shells of *Littorina*, for example, have significantly deeper shells than those growing on flat surfaces (Seed, 1977; see also Stanley, 1970 for *A. simplex*). The pronounced convexity of the upper valve of these anomiiids enables the body to increase in volume without the shell overgrowing the object of attachment to any marked extent. The latter is especially important since the fragile shell margins of these bivalves are particularly vulnerable when exposed. In a series of laboratory experiments, Muntz *et al.* (1965) found that only those *Anomia* where the shell margins projected beyond the substratum were eaten by predators. Table 2 shows that the weight of the lower



TABLE 3

Shell proportions of *A. ephippium* from Strangford Lough<sup>1</sup> (n = 102)

| Height<br>(cm) | Length<br>(cm) | Height<br>Length | Depth<br>(cm) | Height<br>Depth | B. emb <sup>2</sup><br>(cm) | Height<br>B. emb | Total shell<br>(g) | Upper valve<br>(g) | Lower valve<br>(g) | Upper valve<br>Lower valve |
|----------------|----------------|------------------|---------------|-----------------|-----------------------------|------------------|--------------------|--------------------|--------------------|----------------------------|
| 1.0            | 1.27           | 0.79             | 0.19          | 5.26            | 0.37                        | 2.70             | 0.07               | 0.05               | 0.01               | 5.00                       |
| 2.0            | 2.34           | 0.85             | 0.38          | 5.26            | 0.64                        | 3.13             | 0.57               | 0.44               | 0.11               | 4.00                       |
| 3.0            | 3.36           | 0.89             | 0.56          | 5.36            | 0.88                        | 3.41             | 1.99               | 1.51               | 0.43               | 3.51                       |
| 4.0            | 4.34           | 0.92             | 0.74          | 5.41            | 1.10                        | 3.64             | 4.85               | 3.61               | 1.15               | 3.14                       |
| 5.0            | 5.29           | 0.95             | 0.92          | 5.43            | 1.32                        | 3.79             | 9.68               | 7.08               | 2.45               | 2.89                       |
| 6.0            | 6.22           | 0.96             | 1.10          | 5.45            | 1.52                        | 3.95             | 17.01              | 12.28              | 4.54               | 2.70                       |
| 7.0            | 7.13           | 0.98             | 1.28          | 5.47            | 1.72                        | 4.07             | 27.41              | 19.56              | 7.67               | 2.55                       |
| 8.0            | 8.03           | 0.99             | 1.46          | 5.48            | 1.91                        | 4.19             | 41.42              | 29.28              | 12.06              | 2.43                       |

<sup>1</sup> All saddle-oysters were collected from flat rock surfaces.<sup>2</sup> Byssal embayment.

TABLE 4

Growth of *A. ephippium* on the shells of *Littorina littorea* in Strangford L.

| Date (1976)             | April 1   | May 26     | July 1     | August 16               | September 30 |
|-------------------------|-----------|------------|------------|-------------------------|--------------|
| Mean shell              |           |            |            |                         |              |
| Height mm ( $\pm$ 1S.D) | 9.7 (2.0) | 12.3 (1.8) | 15.4 (1.4) | 20.2 (1.5) <sup>1</sup> | 20.2 (2.2)   |
| Range mm                | 7.0-12.8  | 9.3-14.2   | 13.8-17.3  | 17.0-23.5               | 16.5-24.5    |
| number (n)              | 21        | 10         | 10         | 16                      | 12           |

<sup>1</sup> *Anomia* which had settled on flat stones measured  $25.5 \pm 3.8$  mm by this date (n = 10).

valve increases at a significantly faster rate than either shell height ( $b = 3.39$ ) or the weight of the lower valve ( $b = 1.12$ ). The ratio of upper valve weight/lower valve weight thus decreases quite markedly with increase in body size (Table 3). This is perhaps rather surprising and contrary to what one might have predicted since it is the exposed upper valve in anomids which is most vulnerable to the ravages of the environment. Although the byssal embayment does become proportionately smaller as the shell increases in size (Table 2) it seems extremely unlikely that this factor alone would be sufficient to explain the differences in relative growth between the two valves. Perhaps a more plausible explanation should be sought in terms of the mechanical efficiencies of the valves themselves. Dome-shaped shells are intrinsically stronger than flat shells (see Wainwright, 1969). Thus, as *Anomia* increases its body mass and the adductor muscle (which connects the two valves) becomes progressively more powerful, the mechanical stresses imposed on the shell can perhaps be resisted only through a disproportionate increase in the thickness of the flatter, more fragile lower valve.

Table 4 records the seasonal changes in absolute shell height of *Anomia* which had settled extensively on the shells of *Littorina littorea* during 1975. These saddle-oysters averaged 9.7 mm by the end of their first winter when a pronounced check mark was clearly visible around the shell margin.

Rapid growth occurred throughout late spring and early summer until by the end of their second growing season the average size of these anomids was  $20.2 \pm 2.2$  mm. On the basis of such growth rates, and knowing that growth in most bivalves tends to decline gradually with age (Seed, 1980) the largest occurring saddle-oysters in the Strangford population (many of which are well over 6.0 cm) must be quite old. It is interesting to note, therefore, that once beyond a certain size range (c. 3.0 cm) *A. ephippium* in L. Ine were only rarely preyed on by crabs (Muntz *et al.*, 1965).



## ACKNOWLEDGEMENTS

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## REVIEW

*Seashells—Bivalves of the British and northern European Seas.* By J. Møller Christensen. Revised and adapted by S. Peter Dance. 124 pp.—coloured figures. Penguin Books Harmondsworth, 1980. £1.95.

Anything these days with 124 pages, nearly all of which carry several excellent colour illustrations, for £1.95 is undoubtedly good value but this little book is even better value than might appear at first sight.

When I was invited to a party in June, 1978 to launch this series of Penguin Nature Guides I thought—what, yet another series of nature books! Every European publisher of note seems to have initiated such a series, so that there are now literally scores of books to choose from, all dealing with birds, butterflies, fungi, flowers etc. The choice is now literally bewildering in some groups. One sees more books on butterflies than butterflies! Some cover wide fields so thinly that most of what one finds is unlikely to be treated. Others are naive in the extreme, written by folk who do not seem to have noticed that most of the species they deal with are now so rare or virtually extinct that none of their readers has the slightest hope of seeing them—they might have been useful guides at the beginning of last century when perhaps there was an otter on every stretch of river.

This present book sensibly deals with a restricted group from a restricted area thus allowing it to be covered in sufficient detail to make it genuinely useful. This probably limits its general appeal but a more limited number of people will actually be able to use it to name things they find. Like so many modern natural history books it is a product of a united Europe. Written and illustrated originally by Danes, it has been translated by H. W. Lascelles and revised and adapted by Peter Dance (who needs no introduction to Mollusca students in Great Britain because of his own books), set by a firm in Tyne and Wear and printed in Portugal. Whilst politicians argue futilely the scientific and commercial world have their United Europe already.

I have not seen the original Danish edition but I suspect Dance's adaptation has been quite extensive. There are introductory chapters on the morphology, ecology, biology and zoogeography of bivalves but most of the book contains good descriptions of about 150 species accompanied by really adequate illustrations. It deals with fewer species than Tebble's well known work but is less dry and more readable. It's well worth having both works. A very few species not occurring in British waters are also dealt with.

I have not hunted for errors but I would have liked to know the origin of the illustrations used on the end papers which depict an eighteenth century boatman engaged in mussel culture—presumably from some Danish work of that period.

One word about conservation. Amongst the plethora of natural history books spewed out on the public recently, many still have sections on the making of private collections but few mention conservational aspects. Conchology is fortunate in that one can collect dead shells and not have to kill animals. The time for the making of casual collections involving such killing is now definitely past. Many species are now so uncommon that depredations by collectors, formerly of no importance as a limiting factor, now have a serious effect. A stronger stand on conservation by the publishers of natural history books could help considerably.

Although I suspect it is hopeless to try and teach the English any reasonable eating habits I might add that all edible bivalves (infinitely more tasty than gastropods) are much nicer fried in butter or grilled with garlic butter or provençale with tomatoes than just pickled in vinegar! A bit more about which species are worth eating could be added to a future edition.

This book is attractively bound in quite stiff boards and is small and inexpensive enough to be taken into the field. Altogether a commendable effort by all concerned.

B. VERDCOURT



# REPORT ON THE MOLLUSCA COLLECTED BY HUGH SCOTT IN THE GUGHÉ HIGHLANDS (ETHIOPIA), WITH THE DESCRIPTION OF TWO NEW SPECIES OF *GULELLA* (PULMONATA: STREPTAXIDAE)

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(Read before the Society, 17 May, 1980)

*Abstract:* Hugh Scott's small collection of snails made during his expedition to the Gughé Highlands, Ethiopia has been discovered in the British Museum (Natural History). A brief account of it is given and two new species of *Gulella*, *G. (Molarella) hughscotti* and *G. tolaensis* are described. A key to the species of *Gulella* from the Horn of Africa is presented.

When describing new species of *Bocageia* from the Gughé Highlands in Ethiopia I (Verdcourt, 1976) commented on the apparent lack of any material in the British Museum (Nat. Hist.) from these mountains collected by Dr. Hugh Scott. Working on a quite different problem at the Museum, I noticed a box of material collected in the Gughé Highlands during December 1948. Since this was the time the Scott Expedition visited the area, this material must have been collected by it and although no collector's name appears on the boxes the handwriting does appear to be Scott's.

Unfortunately most of the material belongs to genera the species of which cannot be named without a revision, but two species of *Gulella* are described here although based on single specimens. Both the *Bocageia* species I described in 1976 are, as might be expected, represented. The lots are as follows with the field notes repeated more or less verbatim.

- (1) Summit of Mount Gughé, south-west side, ca 11000-12000 ft., at roots of plants, 21.xii.1948. *Vitrina* sp., *Bocageia* (two spp.).
- (2) Mt. Tola, ca. 10000 ft., from humus under bushes near a spring, 11.xii.48, leg. A. Negussie [Scott's caravan leader]. *Bocageia* cf. *aethiopica* Thiele, *Homorus* spp. (2-3), *Vitrina* sp.
- (3) Mt. Tola, ca. 10000 ft., near a spring, 10.xii.48. *Bocageia fusiformis* Verdc.
- (4) Mt. Tola, top, ca. 11000 ft., bog vegetation, 15.xii.48. *Gulella* sp. nov. (see below).
- (5) Mt. Tola, ca. 9500 ft. in rather dry humus under large trees in small patch of forest, 13.xii.48. *Bocageia ovoidea* Verdc., *B. fusiformis* Verdc. (narrow form), *Cerastua* cf. *bambuseti* (von Martens).
- (6) Mt. Tola, top, ca. 11000 ft., from peaty soil beneath moss and grass-tufts, 15.xii.48. *Bocageia* cf. *aethiopica* Thiele.
- (7) Same locality, altitude and date, from peaty soil at roots of plants or from a small bog whence a stream flows over the eastern precipice. *Bocageia fusiformis* Verdc., *B.* cf. *aethiopica* Thiele, *B.* sp., *Vitrina* sp.
- (8) Mt. Tola, ca. 10000 ft., among or beneath roots of ferns and grass-tufts, 18.xii.48, *Bocageia* cf. *aethiopica* Thiele, *Homorus* sp., *Gulella* sp. nov. (see below).
- (9) Mt. Tola, ca. 10000 ft., from humus under bamboo forest, 25.xii.48. *Bocageia ovoidea* Verdc.

For completeness other lots in the same collection from other parts of Ethiopia are listed.

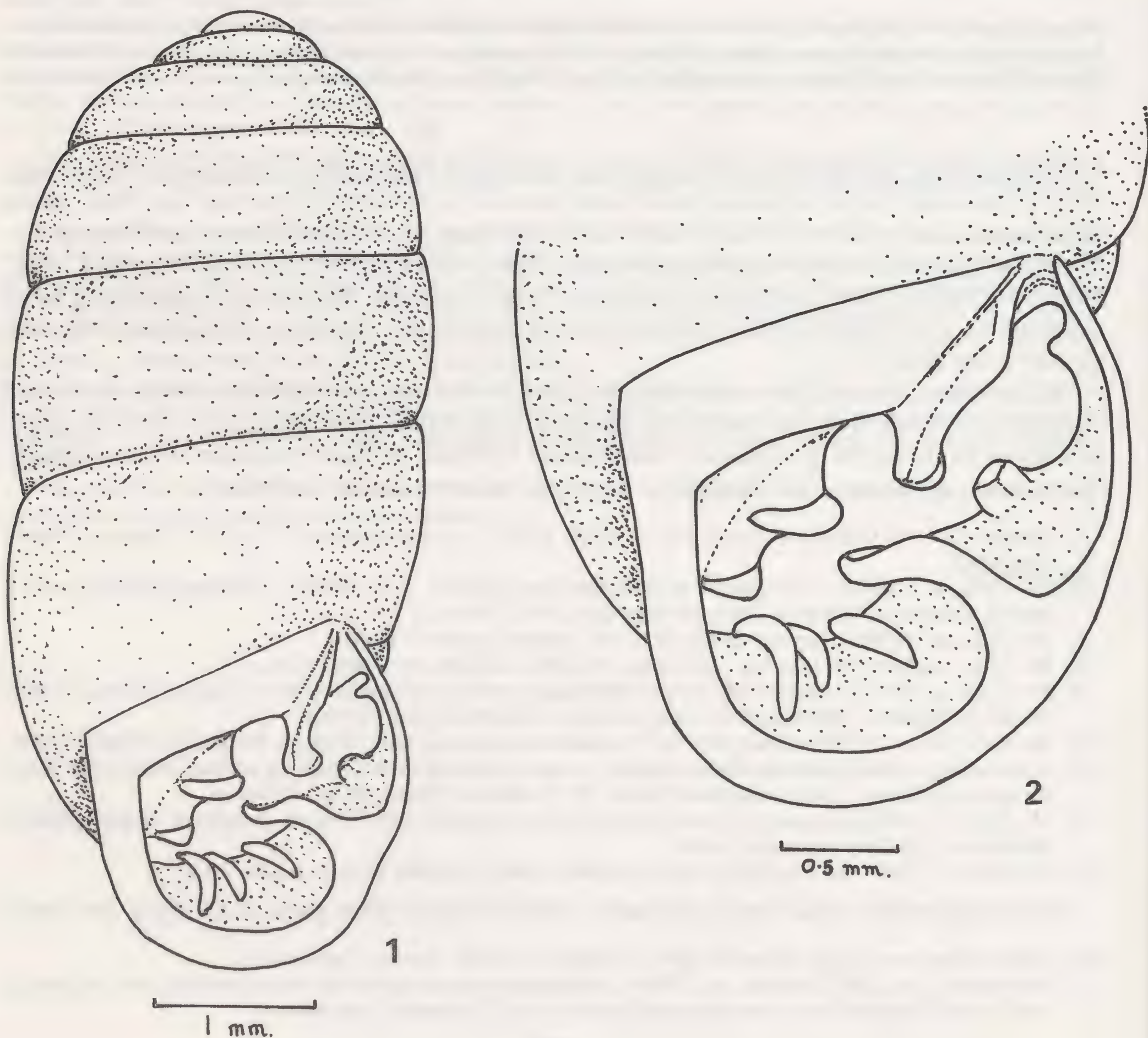
- (10) Walamo Province, Soddu, Menelik's Hill, ca. 6000 ft. 1.xi.48. *Homorus (Subulona)* sp.
- (11) Near Soddu, top of Mt. Darmota, ca. 9000 ft., from damp vegetation beneath earth-bank and trees separating fields several hundred feet below the actual summit; 4.xi.48. *Homorus (Subulona)* sp.



- (12) Same locality and altitude, *Homorus* (*Subulona*) sp. from grass on actual summit, over 9000 ft., *Vitrina* sp. from the rock face of a spring a little below, 5.xi.48.
- (13) Near Soddu, Mt. Damota, 800–1000 ft. below summit, on steep rocky southern face, at roots of coarse grass and other herbage, 6.xi.48. *Homorus* (*Subulona*) sp., *Bocageia* sp.
- (14) Gamo Province, between Chench and Dita, 9000 ft., shells found under leaves of stalkless thistle on bare hillside, 4.xii.48. ?*Vitrina* sp.
- (15) Dita, 8000–9000 ft., damp humus under *Kniphofia*, bracken, etc. *Vitrina* sp. *Bocageia* cf. *aethiopica* Thiele.
- (16) Addis Ababa, under big volcanic boulders in damp soil, 29.xi.48 and one specimen apart from first summit of Mt. Damota, near Soddu, ca. 7500 ft. 28.x.48. *Homorus* (*Subulona*) (two species), *Cerastua* sp. (unfortunately not possible to distinguish which shell was from Damota now).

The family Streptaxidae decreases in importance quite markedly as one moves northwards from East Africa into Ethiopia and the Somali Republic and thence to tropical Arabia. So far only about a score of *Gulella* and *Ptychotrema* species and about 10 of *Tayloria*, *Gonaxis*, *Edentulina* and other genera have been reported. Inadequate collecting may over-emphasize this decrease, but it is undoubtedly real. It was, therefore, with great interest that I discovered the *Gulella* species mentioned above and described below. Despite the inadequacy of the material the species are well-characterized and a key is given to help separate them from other species described from the area.

***Gulella* (*Molarella*) *hughscotti* sp. nov.** Figs. 1, 2.





*Description:* Shell cylindrical with a narrow horizontally placed umbilical slit, probably glossy when fresh (but single specimen very worn), probably pure white; spire produced, the sides straight beneath, convex above, the apex narrowly rounded. Whorls 7, slightly convex, gradually increasing, the sculpture not evident but probably smooth save for very fine close striae immediately behind the peristome; a finely incised spiral line around some parts of the last three whorls is probably an artifact due to wear; suture shallow, not crenellate. Aperture subquadrate, the columella and parietal sides straight and subrectangular, the outer lip curved, the peristome thickened reflected and somewhat sinuous; dentition 7-fold; a strong curved parietal lamella situated close to the right-hand edge, distally reflexed to the right; at the top of the sinus of the outer lip, a small inset tooth; below this in line with the distal margin of the parietal lamella, a larger subangular tooth; yet further down about the middle of the outer wall a sinuously curved entering lamella, the outer end of which merges with the thickened peristome which is outwardly curved in this area; this lamella corresponds to a large pit outside behind the peristome which bears a horizontal impressed line at its base; the basal wall bears three curved inset lamellae, the left-hand one the most marked and the other pair lower and not reaching so close to the peristome; this left-hand lamella corresponds to a similar but smaller pit behind the peristome; the columella bears no external teeth but the fold at the upper angle bears two marked well-separated inwardly entering lamellae.

*Dimensions:* Height 6.2 mm., breadth 2.8 mm., height of aperture 2.2 mm., breadth 2.2 mm.

*Distribution:* Ethiopia, Gamo Province, Gughé Highlands, Mt. Tola, among or beneath roots or ferns and grass-tufts, 10000 ft. (3000 m.), 18 Dec. 1948, H. Scott (holotype in British Museum (Nat. Hist.) no. 198016).

This does not come near any described species known to me or to Dr. van Bruggen who has a good knowledge of the species from southern Africa.

***Gulella tolaensis* sp. nov.** Figs 3, 4.

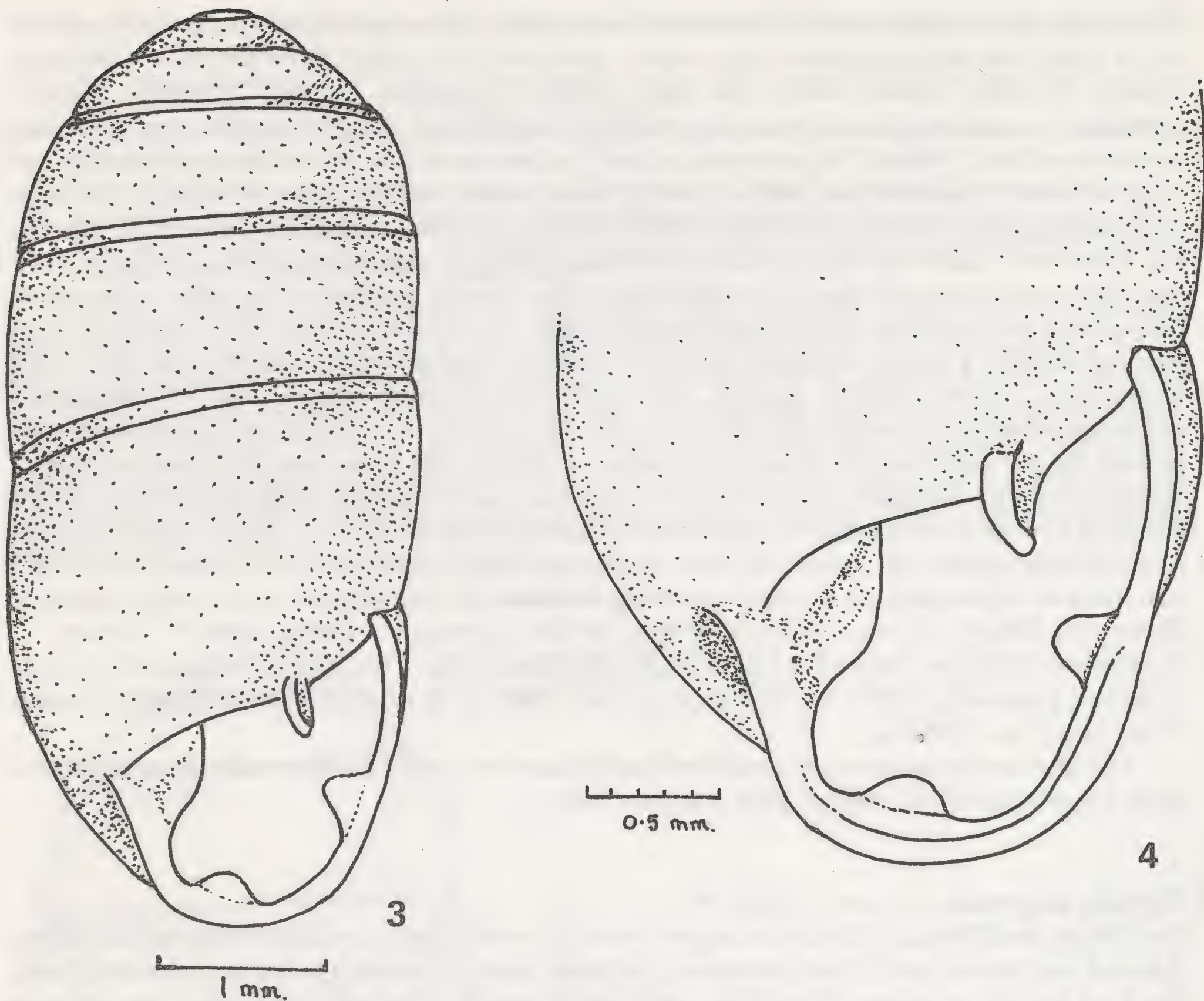
*Description:* Shell shortly cylindrical, imperforate but with a linear umbilical impression, glossy, translucent creamy white; spire produced, the sides more or less straight below, concave above, the apex broadly rounded. Whorls  $6\frac{1}{2}$ , very slightly convex, gradually increasing, smooth save for faint growth lines; last whorl with some obscure striae behind the peristome and some very fine spiral lines only visible at high magnification; suture scarcely impressed, margined, not crenellate. Aperture subquadrate, the parietal, basal and columella walls more or less at right angles, the outer lip smoothly rounded; dentition not obstructing aperture; a rather small thin parietal lamella set at about  $\frac{1}{3}$  the length of the parietal wall from the right-hand edge; a small slightly inset nodular tooth at about the mid-point of the outer wall and a similar tooth rather near the left-hand side of the base, both corresponding with shallow depressions in the outer wall; columella with an inset upper angular fold bearing a thickened margin forming an inwardly entering lamella; peristome thickened, particularly along columella wall.

*Dimensions:* Height 5.4 mm., breadth 2.45 mm., height of aperture 1.9 mm., breadth 1.7 mm.

*Distribution:* Ethiopia, Gamo Province, Gughé Highlands, Mt. Tola, bog vegetation on summit, ca. 11000 ft. (3300 m.), 15 Dec. 1948, H. Scott (holotype in British Museum (Nat. Hist.) no. 198017).

This ordinary looking species is similar to many described species, but not identical with any. Amongst the East African species it will key near to *G. ludwigi* Verdc. & Venmans, but that has a more cylindrical shell with the main part of the spire with 4 whorls not 3; *G. columella* is smaller with a quite different columellar lobe and differently shaped teeth.



KEY TO *GULELLA* OF N.E. AFRICA AND ARABIA

1. Aperture without processes ..... 2  
 Aperture with processes ..... 3
2. Shell 5 × 2 mm. oblong-cylindrical with 5 whorls visible from the front;  
 striate ..... *G. simplicima* (Preston)  
 Shell 8.5 × 2.75 mm., narrowly cylindrical with 9 whorls visible from the front; first 2  
 whorls smooth, rest with diagonal striae (Arabia) ..... *G. schweinfurthii* (Thiele)
3. Columella with bifid process or lobe ..... 4  
 Columellar process not bifid ..... 7
4. Shell larger, striate, 7–8 × 4.5–5 mm.; aperture formula  
 1;2;1;1 + 1(2) ..... *G. somaliensis* (E. A. Smith)  
 Shell smaller ..... 5
5. Labral slab not bifid; shell 6.2 × 2.8 mm., suture not crenellate; aperture formula 1;3;3;L(2),  
 the lowest labral process a deeply entering sinuous curved lamella; columella fold  
 with two well-separated inwardly directed lamellae ..... *G. hughscotti* sp. nov.  
 Labral slab bifid, formula 1;1(2);1;1(2) ..... 6
6. Shell 5 × 2 mm., almost smooth but suture granulate-  
 papillate (Arabia) ..... *G. isseli* (Paladilhe)  
 Shell 7.1 × 3.1 mm.; suture crenellate ..... *G. cecionii* Bacci



# REPORT ON THE MOLLUSCA

7. Aperture formula 1;0;0;0,1;trace;0:0 or 1;1;0;0..... 8  
Aperture with more teeth..... 10
8. Shell tapering cylindrical 7 × 2 mm., finely striate and costulate behind aperture; a single parietal tooth present (Socotra) ..... *G. cylindracea* (E. A. Smith)  
Shell smaller; mainland species ..... 9
9. Dentition reduced to a parietal tooth and a slight thickening on the outer lip; formula 1;trace;0;0; shell 3.9—4.5 × 1.6—1.8 mm., closely costulate  
*G. hemmingi* Verdcourt  
Dentition reduced to a parietal tooth, and a small inset one on the outer lip; formula 1;1;0;0; shell 5.8 × 2.3 mm. with suture crenellate..... *G. abessinica* Thiele
10. Shell large, 12.5 × 5 mm., striate; aperture formula 1;1;2;1, the columella process situated on the inset lobe at angle..... *G. ringens* Piersanti  
Shell smaller..... 11
11. Aperture with labral tooth deeply inset from the peristome; basal tooth inset; columella fold inset, broad, thickened at base and margin; formula 1;1;1;L; shell smooth save for slightly crenellate suture, 6.25 × 2 mm..... *G. meneliki* (Preston)  
Labral tooth not so deeply inset..... 12
12. Shell small, shining, 5.4 × 2.45 mm.; teeth small, not obstructing aperture, 1;1;1;L; columellar fold bearing a thickened margin forming an inwardly entering lamella..... *G. tolaensis* sp. nov.  
Shell larger with different teeth..... 13
13. Aperture with 6–7 teeth, formula 1;3;1;2 (*turennei*) or 1;2;1;1 + 1 (2) or 1;2;1;1 + 1; shell 7–8 × 4.5–5 mm., striate ..... *G. somaliensis* (E. A. Smith)  
(= *turennei* (Neuville & Anthony))  
Aperture with fewer teeth or if with 6 teeth then two very small and the columella one set on the inset lobe ..... 14
14. Formula 1;1;1;1; shell 8–8.5 × 3–4 mm..... *G. somaliensis* var. *megaensis* Piersanti  
Formula 1; trace or 1 + 1 + trace; 1;L, the lobe with a central projection; shell 7.5–8.25 × 3.5, finely striate ..... *G. aethiopica* Thiele\*

\*Type examined at Berlin.

## REFERENCE

- VERDCOURT, B., 1976. Two new species of *Bocageia* Girard from Ethiopia (Mollusca: Subulinidae). *Arch. Molluskenk.* 107: 107–109, figs. 1–3.



## REVIEW

*Süßwassermollusken*. By P. Glöer, C. Meier-Brook and O. Ostermann. 73 pp., text illustrated. Deutscher Jugendbund für Naturbeobachtung, Buchenstr. 18, 2000 Hamburg 60, 1978. Price DM 7.50.

*Mięczaki (Mollusca), Slimaki (Gastropoda). Fauna Śródkowodna Polski, part 7*. By A. Piechocki. 187 pp., text illustrated. Polska Akademia Nauk, Państwowe Wydawnictwo Naukowe, Warsaw & Poznań, 1979. ISSN 0071-4089, ISBN 83-01-01143-2. Price zł 50.00.

*A Víziszigák és Kagylók (Mollusca) kishatározója* [a guide for the identification of Hungarian freshwater Mollusca]. *Vízügyi Hidrobiológia, part 6*. By A. Richnovszky and L. Pintér. 206 pp., text illustrated. VIZDOK, Budapest, 1979. ISSN 0324-2501, ISBN 963-602-162-7.

There seems recently to have been a strong revival of interest in European freshwater Mollusca. These three books offer comprehensive guides to the freshwater faunas of Germany (79 species), Poland (45 species, excluding bivalves) and Hungary (71 species). Brackish-water species are excluded.

The unpretentious little book by Glöer, Meier-Brook and Ostermann is illustrated by photographs, mostly of good quality. Some of the pictures of *Pisidium* are however rather poor and the mixture of SEM and light photographs used here is confusing in cases where surface textures are important for identification. There are brief diagnoses for each species, followed by notes on distribution and ecology. There is an excellent visual key to genera, and a short bibliography. An unusual but useful feature is an appendix giving the localities for every shell illustrated.

Dr. Piechocki's book is much more ambitious, being a monographic treatment of the freshwater gastropods of Poland. Details are included of shells, soft anatomy, reproduction and ecology. The illustrations are excellent, though unfortunately in some cases rather poorly printed so that fine detail is lost. There is a very full bibliography of European scope. This is likely to remain a standard work for the foreseeable future.

The book by Richnovszky and Pintér is simpler in intention, being primarily an identification-guide for the Hungarian species, based on shells. Also included are a few species unknown in Hungary but likely to be found there (e.g. *Pisidium hibernicum*, *P. pulchellum*). The drawings are mostly outlines, rather rough, but workmanlike and useful. Very full details of geographical distribution in Hungary are given. There is a bibliography.

All three works contain check-lists and keys, and are indexed.

It is interesting to compare the lists of species recognized in each country. The majority are common palaearctic forms, such as are familiar in the British Isles. *Potamopyrgus jenkinsi* now occurs widely. *Ferrissia wautieri* is recognized in Germany and Hungary, and is described for Poland in anticipation of its likely discovery in that country. But there are also important regional differences. In central and south Germany the genus *Bythiospeum* (family Hydrobiidae) is met with, virtually endemic to the caves and springs of that area. Following the work of Bolling (*Naturf. Ges. Bamberg* 40, p. 21), some forty described species are now reduced to three only, though these remain ill-defined and the last word has certainly not been said on these difficult snails. In Hungary we find no fewer than four species of *Theodoxus*, and many unfamiliar operculates (*Sadleriana*, *Fagotia*, *Melanopsis*, *Amphimelania*). Other differences are more apparent than real. There are differences of opinion as to the number of species to be included in *Gyraulus* and *Anisus* (family Planorbidae). An old unresolved puzzle concerns the exact taxonomic status of *spirorbis* L., *leucostoma* Millet and *septemgyratus* Rossmässler (here mostly accepted as good species) within the *Anisus* complex. Similarly, *Lymnaea (Galba) palustris* is sometimes thought to be a complex of species (*corvus* Gmelin, *turricula* Held, *occulta* Jackiewicz), a view accepted by Piechocki and by Glöer *et al.*, but resisted by Richnovszky and Pintér.

M. P. KERNEY



# A STUDY OF THE DIETS OF SOME BRITISH FRESHWATER GASTROPODS

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(Read before the Society, 17 May, 1980)

*Abstract:* Gut contents were examined in 20 British species of freshwater gastropods. All showed a wide range of diet, with detritus forming the bulk of the food. Algae rarely formed over 25% of the food ingested, fresh macrophytes were rare, and animal remains were insignificant. *Planorbarius corneus* grew most on a varied diet, then on a eutrophic detritus, and least on an oligotrophic detritus. Diet preference was shown, in the laboratory, and *Elodea canadensis* (Canadian Pondweed) was rejected by some species. Some of the smallest pulmonates and the benthic prosobranchs lacked sand grains in the gut. *Gyraulus albus* was not attracted to an algal food source.

In the past the study of aquatic gastropod diets has lacked critical experimental data, and conflicting results have been reported in Gaevskaja (1966). Frömming (1956), summarizing results before that date, stated that most species ingested a wide range of foods which included bacteria, fungi, algae, and macrophytes. He concluded that only a few species require animal protein, but showed for six pulmonates that there was an increased rate of growth and reproduction when an algal or macrophytic diet was supplemented by animal protein. Numerous authors stressed the nutritional importance of a range of different foods, that is to say, a balanced diet. Over 50 species of gastropods ingested 17 different food items which included detritus, bacteria, yeasts, algae, lichens, fallen tree leaves, decayed macrophytes, animal remains and living invertebrates.

The reported ingestion by four prosobranch species of Oligochaeta and Porifera may have been accidental as they are mainly sediment feeders, but experimental verification is needed. In view of the abundance of uncritical observations, and the importance of gastropods in the food web, the author decided to study diets by examination of gut contents and simple experimental procedure.

## MATERIALS AND METHODS

1. *Analysis of alimentary tracts of natural snail populations.* The habitats and localities from which 20 species of freshwater snails were collected are shown in Table 1. From February to August 1970, 20 species were removed with a pond net from a range of water bodies in N.W. England. Twenty-five individuals of each species were taken from each site where possible. The larger freshly collected snails were instantly placed in a 15% formalin solution and the smaller ones deep frozen in dry ice, to arrest digestion of the gut contents. Deep frozen snails were later thawed out, which enabled the rapid removal of viscera as the columellar muscle was relaxed.

The guts of the larger snails were dissected out after breaking the shell; those of the smaller snails were dissected out and mounted in glycerine. However, snails less than 10 mm shell length



TABLE 1.  
Collection sites for water snails

| Locality               | County          | Grid reference | Date               | Type of water body      | Nutrient status | Hardness | Gastropod species collected                                                                                                                                                                                                                                                           |
|------------------------|-----------------|----------------|--------------------|-------------------------|-----------------|----------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Wirral pond 1          | Cheshire        | SJ 234893      | 28.1.70<br>3.7.70  | Lowland pond            | High            | High     | <i>Bithynia tentaculata</i> , <i>Lymnaea peregra</i> , <i>L. palustris</i> , <i>Planorbis carinatus</i> , <i>P. vortex</i> .                                                                                                                                                          |
| Wirral pond 4          | Cheshire        | SJ 259856      | 20.2.70            | Lowland pond            | High            | High     | <i>Planorbis vortex</i> , <i>P. albus</i> , <i>P. corneus</i> , <i>Segmentina complanata</i> .                                                                                                                                                                                        |
| Wirral pond 5          | Cheshire        | SJ 289842      | 20.2.70            | Lowland pond            | High            | High     | <i>Lymnaea peregra</i> .                                                                                                                                                                                                                                                              |
| Wirral pond 9          | Cheshire        | SJ 325814      | 5.2.70             | Lowland pond            | High            | High     | <i>Lymnaea stagnalis</i> , <i>L. peregra</i> , <i>Planorbis corneus</i> , <i>P. crista</i> .                                                                                                                                                                                          |
| Wirral pond 13         | Cheshire        | SJ 324805      | 28.1.70<br>3.7.70  | Lowland pond            | High            | High     | <i>Lymnaea palustris</i> , <i>Planorbis corneus</i> , <i>P. albus</i> , <i>P. vortex</i> .                                                                                                                                                                                            |
| Wirral pond 15         | Cheshire        | SJ 318795      | 28.1.70            | Lowland pond            | High            | High     | <i>Lymnaea peregra</i> .                                                                                                                                                                                                                                                              |
| Wirral pond 29         | Cheshire        | SJ 333814      | 5.2.70             | Lowland pond            | High            | High     | <i>Lymnaea peregra</i> , <i>Planorbis crista</i> .                                                                                                                                                                                                                                    |
| Wirral pond E1         | Cheshire        | SJ 591808      | 20.2.70            | Lowland pond            | High            | High     | <i>Lymnaea peregra</i> .                                                                                                                                                                                                                                                              |
| Wirral pond E2         | Cheshire        | SJ 591808      | 20.2.70            | Lowland pond            | High            | High     | <i>Lymnaea peregra</i> , <i>Planorbis vortex</i> , <i>Physa fontinalis</i> .                                                                                                                                                                                                          |
| Wirral pond J          | Cheshire        | SJ 566798      | 20.2.70            | Lowland pond            | High            | High     | <i>Lymnaea peregra</i> .                                                                                                                                                                                                                                                              |
| Birkenhead Park pond   | Cheshire        | SJ 311891      | 10.1.70<br>29.6.70 | Lowland pond            | High            | High     | <i>Bithynia tentaculata</i> , <i>Potamopyrgus jenkinsi</i> , <i>Lymnaea peregra</i> , <i>Planorbis albus</i> , <i>P. corneus</i> .                                                                                                                                                    |
| Fender Valley pond     | Cheshire        | SJ 291859      | 11.4.70            | Lowland pond            | High            | High     | <i>Lymnaea palustris</i> , <i>Planorbis crista</i> .                                                                                                                                                                                                                                  |
| Crooksmoor reservoir   | Yorkshire       | SK 338874      | 8.67               | Small boating reservoir | High            | Low      | <i>Potamopyrgus jenkinsi</i> .                                                                                                                                                                                                                                                        |
| Llyn Nantle            | Caernarvonshire | SH 517532      | 23.4.70            | Mountain lake           | Low             | Low      | <i>Potamopyrgus jenkinsi</i> , <i>Lymnaea peregra</i> , <i>Ancylus fluviatilis</i> .                                                                                                                                                                                                  |
| Lake Dwythwch          | Caernarvonshire | SH             | 14.4.70            | Mountain lake           | Low             | Low      | <i>Lymnaea peregra</i> .                                                                                                                                                                                                                                                              |
| Massam's Slack North   | Lancashire      | SD 281099      | 5.70               | Sand dune ditch         | Low             | High     | <i>Potamopyrgus jenkinsi</i> .                                                                                                                                                                                                                                                        |
| Tannyrallt Road        | Caernarvonshire | SH 472520      | 26.4.70            | Roadside ditch          | Low             | Low      | <i>Lymnaea peregra</i> , <i>L. truncatula</i> .                                                                                                                                                                                                                                       |
| Formby Bypass          | Cheshire        | SD 307049      | 8.5.70             | Roadside ditch          | High            | High     | <i>Lymnaea peregra</i> , <i>Aplexa hypnorum</i> .                                                                                                                                                                                                                                     |
| Shropshire Union Canal | Cheshire        | SJ 390710      | 7.4.70<br>10.8.70  | Canal                   | High            | High     | <i>Viviparus viviparus</i> , <i>Valvata piscinalis</i> , <i>V. macrostoma</i> , <i>Bithynia tentaculata</i> , <i>Lymnaea stagnalis</i> , <i>L. peregra</i> , <i>Planorbis carinatus</i> , <i>P. vortex</i> , <i>P. corneus</i> , <i>Physa fontinalis</i> , <i>P. heterostrophus</i> . |
| Grand Union Canal      | Warwickshire    | SP 364644      | 19.4.70            | Canal                   | High            | High     | <i>Lymnaea auricularia</i> , <i>L. peregra</i> .                                                                                                                                                                                                                                      |
| Tannyrallt Stream      | Caernarvonshire | SH 477521      | 26.4.70            | Upland stream           | Low             | Low      | <i>Potamopyrgus jenkinsi</i> , <i>Lymnaea peregra</i> , <i>Ancylus fluviatilis</i> .                                                                                                                                                                                                  |
| Tributary of above     | Caernarvonshire | SH 481521      | 26.4.70            | Upland stream           | Low             | Low      | <i>Ancylus fluviatilis</i> .                                                                                                                                                                                                                                                          |
| River Lowther below    | Westmorland     | NY 561135      | 11.2.70            | Upland stream           | Low             | Low      | <i>Ancylus fluviatilis</i> .                                                                                                                                                                                                                                                          |
| Wet Sledale Reservoir  |                 |                | 23.6.70            |                         |                 |          | <i>Lymnaea peregra</i> , <i>Ancylus fluviatilis</i> .                                                                                                                                                                                                                                 |

Nomenclature follows Kerney, 1976.



were crushed gently, thus the shell fragments could be removed with forceps, and the gut then flooded with glycerine and squashed gently with a cover slip. Each gut squash was scored for diet items using a binocular microscope at  $\times 40$  magnification. The diet items were expressed as a percentage of the total squashed gut area. This index was considered equivalent to the percentage composition of ingesta by gut volume. Algae in the gut contents were identified to the genus or order, and any items forming less than 1% of the diet were omitted from the results.

2. *Chemotactic response to algae*. Three clear plastic tanks each  $30 \times 20 \times 20$  cms were filled to a depth of 5 mm with tap water which had stood for 24 hours. A specimen tube was inverted just underneath the water surface by a clamp stand. One tube was filled with a mixed unicellular chlorophyte algal culture (*Chlorella* sp., *Ankistrodesmus* sp. and *Scenedesmus* sp.), a second with a mixed filamentous chlorophyte algal mass (*Vaucheria* sp. and *Oedogonium* sp.), a third was used as a control and filled with tap water. Any organic diffusate could leak out through the fine mesh nylon covering the specimen tube. Twenty mature *Gyraulus albus* were starved for 48 hours then introduced into each tank.

To maintain any potential diffusion gradient, a cover was placed over each tank in order to prevent air currents affecting the water. The tanks were placed out of direct sunlight to prevent heating and phototactic movement of snails or algae. It would be expected that if the snails were positively chemotactic (i.e. attracted to a smell or taste) to any organic diffusates they would in time move directionally towards the food source. In order to detect any behavioural response of the snails each tank was placed over numbered squares and the position of each snail scored after 12 hours. Three trials were run and no aggregation was detected at either ends of the tanks or near the tubes.

3. *Diet choice experiments*. In order to assess whether there was any selective choice of diets, natural substrates containing snails were isolated, scraped with a scalpel, and percentage composition of scraped substrates compared with gut percentage compositions. No pattern was detected, possibly because of high algal species diversities, discontinuous feeding behaviour on a given substrate, or lack of proper experimental design. This is a technique which should be much refined before any conclusions can be drawn.

Table 2 shows the laboratory experiments that were used to test for selective or indiscriminate feeding. Five snail species were presented with single and multiple choice algal diets both from as wide a range as possible. The snails used were: *Vivaparus vivaparus*, *Bithynia tentaculata*, *Lymnaea peregra*, *Physa fontinalis*, and *Gyraulus albus*. The algal diets used were: a unicellular chlorophyte *Chlorella* sp., a filamentous chlorophyte, *Oedogonium* sp., a filamentous cyanophyte *Oscillatoria* sp. and diatoms *Navicula* sp.

Excessive amounts of algae were placed in a petri dish with ten snails of each species and two replicates were run per feeding trial. Snails were starved for 48 hours in each petri dish prior to the experiments then the algal diets were introduced for 48 hours after which all the snails were removed and deep frozen. The guts were pulled out with a dissecting needle, mounted, squashed and examined to check on ingestion of diet items and to see whether the items were whole or macerated. Fifty faeces from each petri dish were mounted in glycerine, squashed, and scored for the algal diets. Two pieces of a macrophyte *Elodea canadensis* were placed into petri dishes, and 48 hours later faecal squashes were examined for fragments of the plant. Then the macrophytes were examined under the binocular microscope for evidence of radulation of fresh or decayed parts.

4. *Growth responses on different diets*. Detritus predominated in the gut contents of all twenty species from natural habitats. To test whether detritus was the most important diet item, the following experiment was performed. *Planorbarius corneus* was bred in the laboratory, and the young snails reared on three different diet regimes.



TABLE 2

Diet choice feeding trials, based on gut and faecal examinations

| Available diets            | <i>Viviparus viviparus juveniles</i>                                   | <i>Bithynia tentaculata</i>            | <i>Lymnaea peregrea</i>                                                  | <i>Planorbis albus</i>                                           | <i>Physa fontinalis</i>                  |
|----------------------------|------------------------------------------------------------------------|----------------------------------------|--------------------------------------------------------------------------|------------------------------------------------------------------|------------------------------------------|
| 1. Unicellular Chlorophyta | Faeces packed solid with intact cells.                                 | Faeces packed solid with intact cells. | Faeces packed solid with intact cells.                                   | Faeces packed solid with intact cells.                           | Faeces packed solid with intact cells.   |
| 2. Filamentous Chlorophyta | Very occasionally in faeces.                                           | Broken and intact Filaments.           | Macerated, broken and intact Filaments.                                  | A few single cell sporelings only. No Filaments or broken cells. | Broken and intact Filaments.             |
| 3. Filamentous Cyanophyta  | Mostly macerated.                                                      | Trichomes present.                     | Approximately equal amounts macerated & intact Trichomes. Both ingested. | Mostly macerated, a few intact Trichomes.                        | Mostly macerated Trichomes. Rest intact. |
| 1 and 2                    | 1 intact. 2 sporelings only. No evidence of larger parts of Filaments. | Both ingested.                         | Both ingested.                                                           | A few single cell sporelings of 2 packed with 1 intact.          | Both ingested, only 2 macerated.         |
| 1 and 3                    | 1 intact, Cyanophyte trichomes macerated and intact.                   |                                        | Both ingested.                                                           | Both ingested, 3 macerated, a few intact.                        | Both ingested.                           |
| 2 and 3                    | 3 Macerated and intact. No evidence from faeces of 2 ingestion.        | Mostly macerated 3, 2 occasional.      | Both ingested.                                                           | 3 mostly macerated, 2 rare, then sporelings.                     | Both macerated and intact.               |
| 1, 2 and 3                 | 2 not ingested, other two were.                                        | Only 1 abundant, other two occasional  | All three ingested.                                                      | 2 not ingested, 3 macerated and intact Trichomes.                | All three ingested.                      |



## DIETS OF SOME BRITISH FRESHWATER GASTROPODS

1. A varied diet of detritus from a eutrophic pond, decayed leaves, fresh *Elodea canadensis*, a filamentous chlorophyte *Oedogonium* sp. and dead aquatic gastropods. (Water with high nutrient levels and high organic production.)
2. Detritus from Birkenhead Park pond, a hard water eutrophic pond. (Water with high nutrient levels and organic production.)
3. Detritus from Wet Sledale Reservoir, a soft water oligotrophic reservoir. (Water with low nutrient levels and organic production.)

These three regimes were replicated eight times. Twenty-five 2 litre conical flasks were filled with 1.5 litres of Liverpool tap water. Each flask had 20 ml of detritus and a spatula of sand, the latter for diet maceration by the snail gizzard. The eutrophic detritus was black and slightly foul smelling and the oligotrophic detritus was brown and peaty. Both types were sieved through a 1.0 mm mesh, autoclaved to kill algae and stored in a fridge at 5°C. Twenty 1.0 mm juveniles were pipetted into each flask, which was then covered with tin foil. The diameter of each snail was measured at fortnightly intervals for 13 weeks after introduction. The contents of each flask were poured into a large white enamel tray. The detritus was poured back and the juvenile snails stuck to the tray. They were pipetted into a petri dish placed over millimetre graph paper, and the diameter was measured to the nearest half millimetre under a binocular microscope.

## RESULTS

1. *Evidence for a range of diets.* Figs. 1 and 2 show that most species of aquatic snails examined ingest a varied diet of algae, detritus, larger plant fragments (macrophytes) and animal remains. The larger the sample of snails examined the more accurate is the assessment of the diet range. Concerning the frequency of occurrence of diet items in the different species, Fig. 3 shows the following trend in decreasing order: detritus, sand grains, unicellular chlorophytes, diatoms and filamentous chlorophytes, cyanophytes and pyrrophytes, heterokonts, and rhodophytes.

Animal remains are excluded as they formed less than 1% of the diet. This frequency of occurrence would be expected if the ingestion of diet items was non selective.

Fig. 1 shows the following order of decreasing percentage composition of diet items: detritus, sand grains, diatoms and unicellular chlorophytes, other algae, animal remains. This agrees with the frequency of occurrence of these diet items, see Fig. 3. Fig. 4 also shows that *Planorbarius corneus* grew faster on a varied diet compared with a purely detritus diet.

2. *Evidence for animal remains in the diet.* Fig. 3 shows that the maximum percentage frequencies of animal remains occur in the larger pulmonates, *Lymnaea stagnalis*, *L. peregra*, *L. palustris* and *P. corneus*. The minimum percentage frequencies occurred in the smaller species: *Anisus vortex*, *B. tentaculata*, *Potamopyrgus jenkinsi* and *Ancylus fluviatilis*. Probably the increased frequency of animal remains in the larger snail guts is a reflection of their larger mouths.

Bovbjerg (1968) demonstrated positive chemotaxis by four species of lymnaeids, including *Lymnaea stagnalis*, to chopped animal material and Wilbur (1964) said that chitinases were widespread in terrestrial gastropods, although not yet shown to occur in aquatic gastropods. With respect to seasonal change in diet, February and Midsummer samples showed maximum occurrence of animal remains, possibly due to maximum production of invertebrates in Midsummer.

3. *Evidence for a macrophytic diet* (Larger plants above the evolutionary level of algae). Fig. 3 shows that fragments of macrophytes occur most frequently in *L. stagnalis*, *L. palustris* and *P. corneus*.



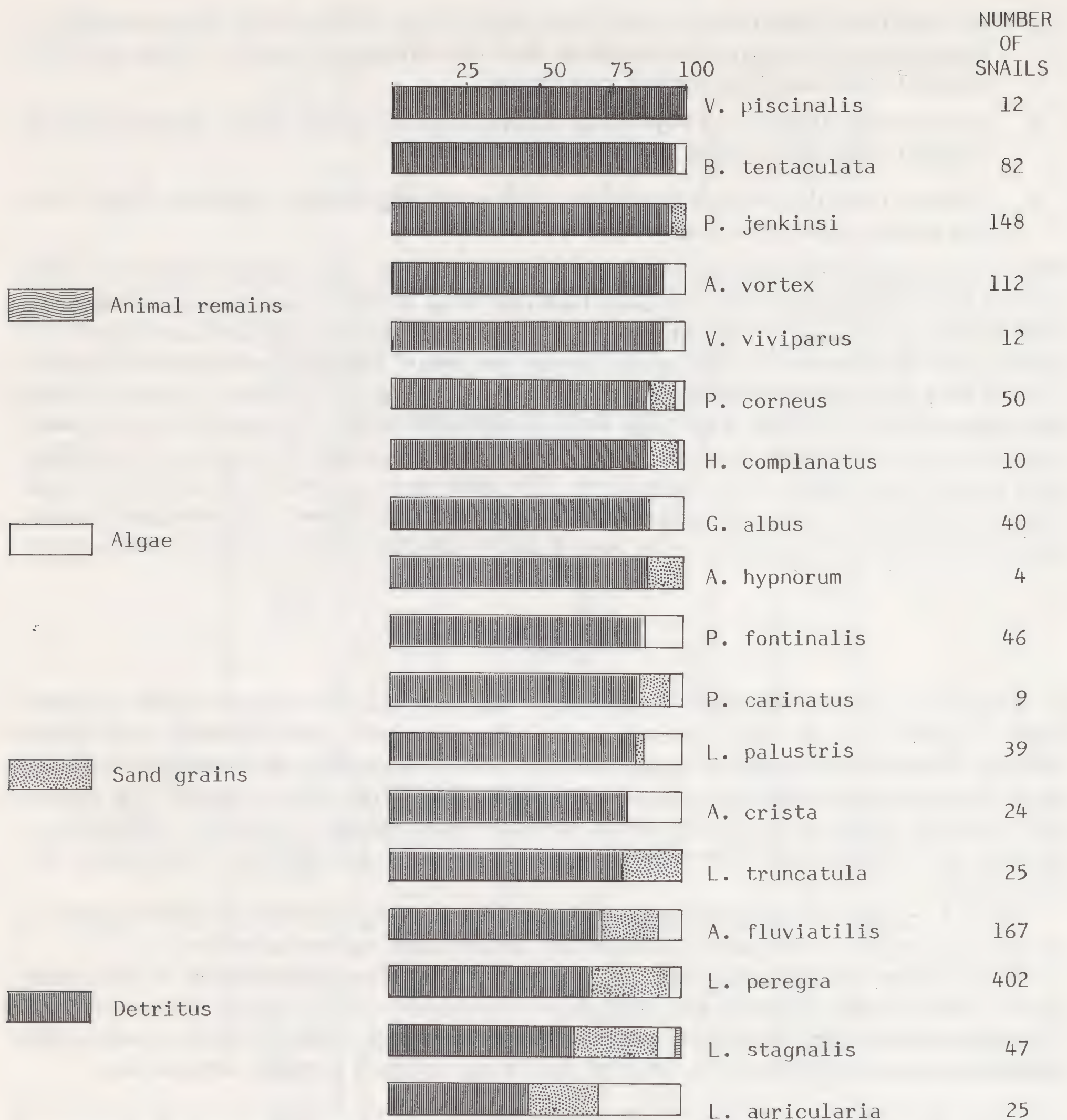


FIG. 1 PERCENTAGE COMPOSITION OF DIETS IN TOTAL SAMPLE OF SNAILS WITH FULL GUTS FROM ALL WATER BODIES.

These species occur more frequently in marginal reedswamp vegetation than *L. auricularia* or *L. peregra*, which are also found on sediments. The larger snails can more easily chew up and ingest parts of macrophytes than the smaller planorbids or physids. Minimum occurrence of macrophytic fragments was found in *L. peregra*, *A. fluviatilis*, *G. albus*, *A. vortex*, *Physa fontinalis*, *Potamopyrgus jenkinsi*, *B. tentaculata* and *V. viviparus*. These species are not confined to macrophytes, and the smaller planorbids are reported to be predominantly periphyton grazers, (i.e. to eat the microscopic community of bacteria, algae, protozoa and diploblasts forming a film on all submerged substrates). The prosobranchs are predominantly sediment dwelling snails. Frömming (1956), discussing the palatability of various macrophytes, says that *Elodea*



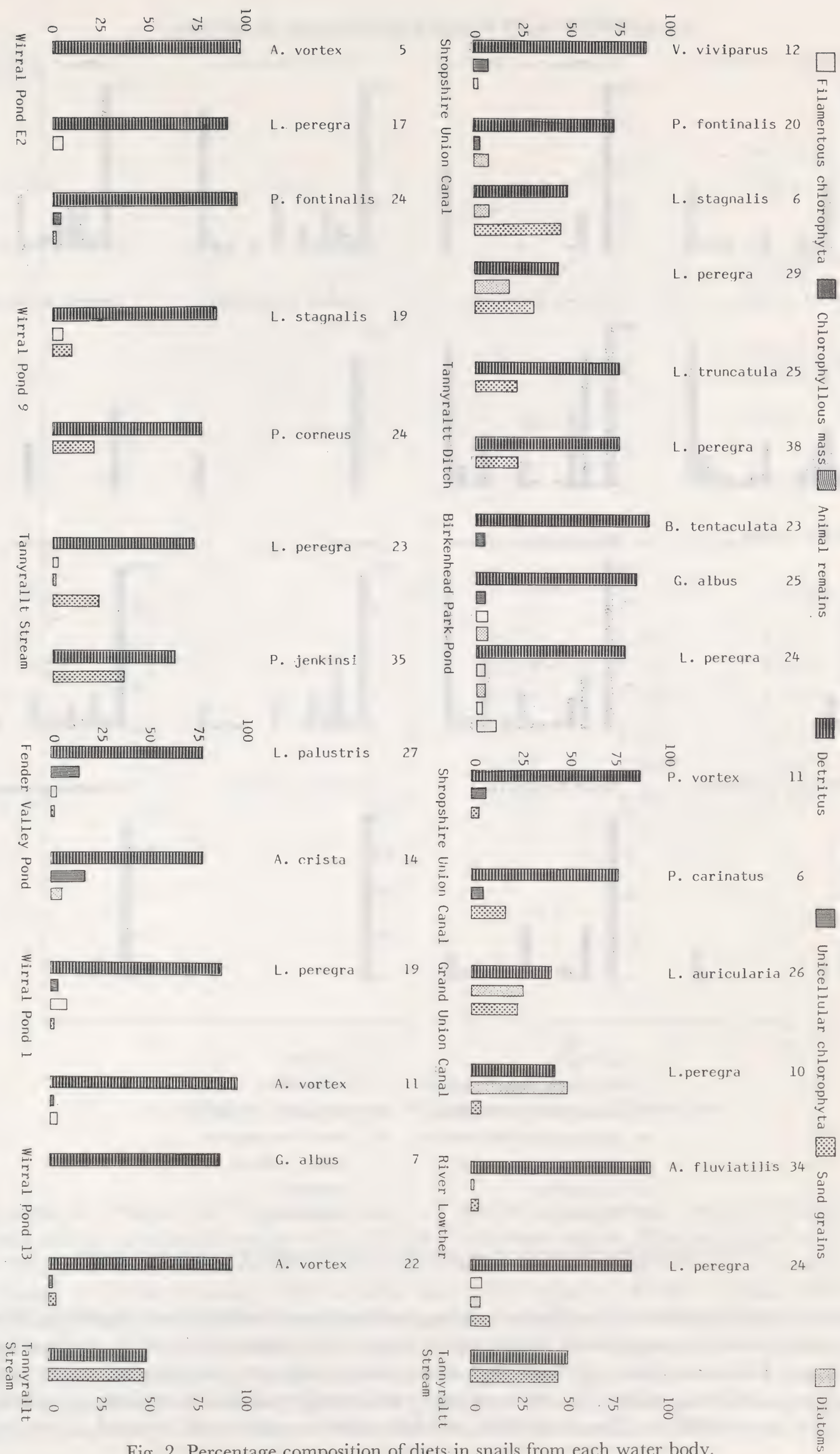


Fig. 2. Percentage composition of diets in snails from each water body.





Fig. 3. Percentage frequency of occurrence of diets in snails from all water bodies.

*canadensis* is rarely eaten and, as Table 1 shows, was only eaten when it was decaying. However both fresh and decaying *Lemna trisulca* (duckweed) were eaten by both *V. viviparus* and *B. tentaculata*. This underlines the fact that many snails will eat macrophytes under artificial laboratory conditions, although they may rarely do so under natural conditions, i.e. when other diet items are available. Therefore field and laboratory studies must be used in conjunction.



# DIETS OF SOME BRITISH FRESHWATER GASTROPODS

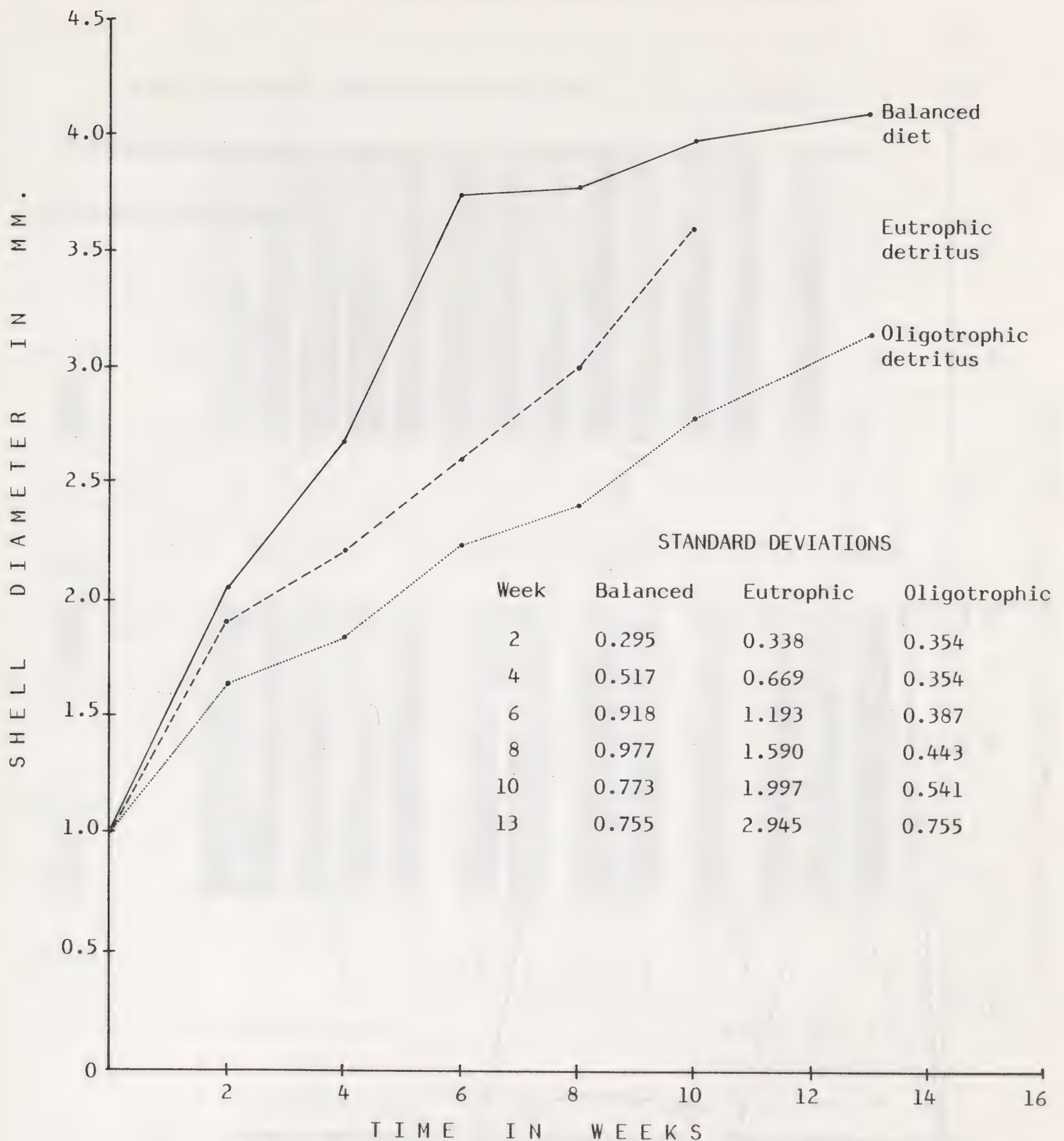


Fig. 4. Growth response curves of *Planorbarius corneus* on different diets

4. *Evidence for an algal diet.* Fig. 2 shows that all species eat a certain amount of algae, with diatoms and unicellular chlorophytes forming the dominant groups. However algae rarely form over 50% of the diets of the freshwater snails studied. The results of algal diet choice experiments are shown in Table 2 using single, double and treble choices. All five species fed on the unicellular chlorophyte *Chlorella*, and the filamentous cyanophyte *Oscillatoria*. Both *G. albus* and *V. viviparus* refused the filamentous chlorophyte *Oedogonium*. *B. tentaculata* showed a preference order of *Chlorella*, *Oscillatoria*, *Oedogonium*, while *L. peregra* and *P. fontinalis* ate all the algal choices without apparent selection. Feeding trends on algae possibly reflect the microhabitat of the snail species, availability of diet items on the substrate, and the diameter of the mouth.





Fig. 5. Growth rate of *Planorbarius corneus* on different diets.

5. *Evidence for a bacterial diet.* The guts of *L. peregra* contain more filamentous bacteria than those of the other species. This may be due to the greater sample size for this species, thus including a greater number of the rarer diet items. Other bacterial forms are more difficult to detect.

Rodina (1948) grew gastropods on bacteria alone, thus demonstrating their nutritional importance and Calow (1974), while citing numerous authors who reported bacterial diets, showed that *P. contortus* preferred detritus with live bacteria.

6. *Evidence for a detrital diet.* For all the species examined the most frequent diet item, in occurrence and percentage composition, is detritus, as shown in Figs. 1, 2 and 3. However the



# DIETS OF SOME BRITISH FRESHWATER GASTROPODS

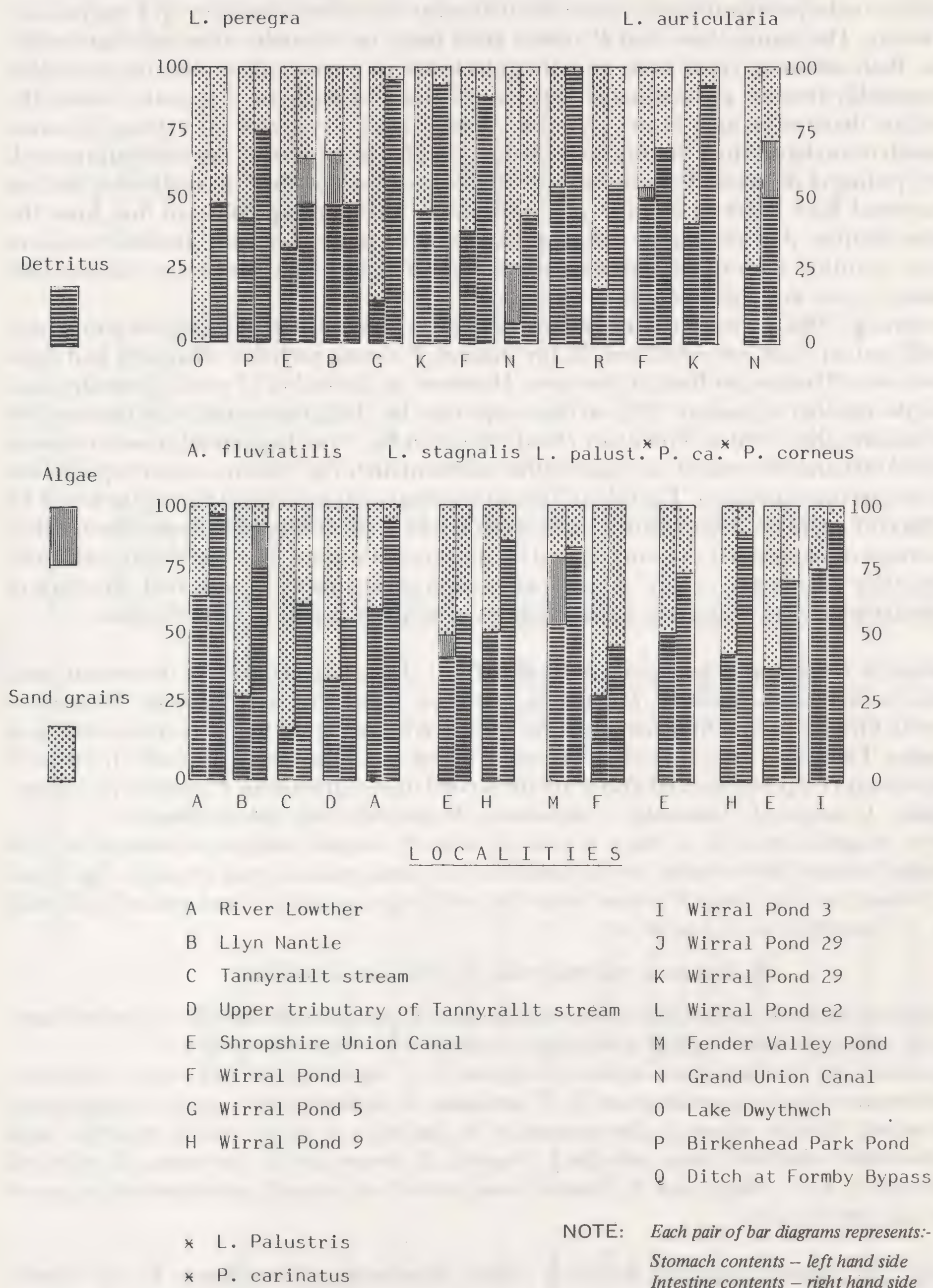


FIG. 6 PERCENTAGE COMPOSITION OF DIETS IN THE STOMACH AND INTESTINE OF SOME SNAIL SPECIES.



sediment-dwelling prosobranchs ingest the maximum percentage of detritus. Fig. 1 shows that there is a trend for an increase in detritus intake from the larger Lymnaeidae, through the Planorbidae to the prosobranchs. *P. corneus* was fed and grown in the laboratory on a detritus diet for 13 weeks. The results show that *P. corneus* grew faster on eutrophic than on oligotrophic detritus. Both sediment types were initially autoclaved to remove algae, but the eutrophic detritus quickly became contaminated with unicellular Chlorophyta. The water above the oligotrophic detritus became brown in colour, probably as a result of the release of humic compounds from the detritus. Snails grown on this type of detritus showed the minimum growth rate with pitting of the shells. Possibly the growth rate was lower because the snails were feeding on a bacterial flora lower in biomass and different in species composition to that from the eutrophic detritus. Also the humic diffusates may have complexed-out the available calcium ions thus retarding the rate of shell formation. Macan (1963) says that many authors find polyhumic waters are unfavourable to gastropods.

Frömming (1956) showed maximum growth rates on a varied diet, although his sample size was small and no replicates were used. In my trials on *P. corneus* each diet treatment had eight replicates with 20 snails per flask at time zero. However, at the end of 13 weeks, mortality had reduced the number of snails by 65% on the varied diet, by 100% on eutrophic detritus and by 81% on oligotrophic detritus. Trends are clearly shown in Fig. 4, with maximal growth response on a varied diet and minimal on an oligotrophic sediment diet. Fig. 5 shows a more rapid initial growth rate on the varied diet. The initial 20 ml of detritus was not replaced during the whole 13 weeks thus the rapid drop in growth rate between weeks 5 and 6 may have been due to either food shortage or an internal rhythm induced by the onset of winter. The snails were seen to be recycling their own faeces, i.e. an 'energetically closed environment' was created. The lack of constant detritus input may have minimized the growth potential on different diets.

7. *Evidence for the presence of sand grains in the diet.* Fig. 1 shows sand grains are the second most frequent diet item in *A. fluviatilis*, *L. stagnalis*, *L. peregra*, *L. palustris* and *P. corneus*. The author agrees with Frömming (1956) in naming these species as ingesting the highest concentrations of sand grains. The lowest frequency of occurrence is found in *G. albus* and *P. fontinalis*. In terms of diet percentage composition, sand grains are the second most common for *P. carinatus*, *P. corneus*, *L. stagnalis*, *L. peregra*, *L. truncatula*, *L. auricularia*, *A. fluviatilis* and *Aplexa hypnorum*.

Few or no grains occur in *A. vortex*, *A. crista*, *G. albus*, *P. fontinalis* and the prosobranchs. This is probably because their mouths are too small for most sand grains to pass through. Fig. 6 and Table 3 show that the stomach is most often the concentration site for sand grains in all snail species. A concentration quotient of

$$\% \text{ Stomach concentration} / \% \text{ Gut concentration}$$

was calculated for each species. Maximum concentration quotients occurred in *A. fluviatilis* and *L. peregra*, although there is great interhabitat variation between the species.

Maximum gut concentrations of sand are shown by *L. stagnalis*, *L. peregra*, and *L. auricularia* and maximum stomach concentrations by *P. carinatus*, *A. fluviatilis* and *L. peregra*. Sand grains always exceed detritus volume in the stomach of *A. fluviatilis*, *L. peregra* and *L. palustris*. Sand grains exceeded other diet items only for *L. stagnalis*, *L. peregra* and *L. truncatula*, all collected from sediments. In *P. jenkinsi* and *A. fluviatilis* some individuals showed equal concentrations of sand grains and detritus.

8. *Evidence for positive chemotaxis.* Bovbjerg (1968) demonstrated movement by the North American *Lymnaea stagnalis* towards animal protein, but not towards plant material. Results of my experiments on diet choice in Table 2 showed that only *V. viviparus* refused any diet. The larger filaments of *Cladophora* and *Vaucheria* were probably too large to pass through the mouth, although finer chlorophyte filaments were ingested. Fig. 2 shows that there are interspecific



TABLE 3

Concentration quotients of ingesta in the stomach of some species

| DIETS OF SOME BRITISH FRESHWATER GASTROPODS |                                      |         |                                      |              |                                    |       |                                             |  |                          |
|---------------------------------------------|--------------------------------------|---------|--------------------------------------|--------------|------------------------------------|-------|---------------------------------------------|--|--------------------------|
| Species                                     | Locality                             | Date    | + Percentage compositions in stomach |              | Concentration quotients in stomach |       | Percentage compositions of other categories |  | No. of stomachs examined |
|                                             |                                      |         | O.D.                                 | S.G.         | O.D.                               | S.G.  |                                             |  |                          |
| <i>Ancylus fluviatilis</i>                  | R. Lowther                           | 11.2.70 | 65.8<br>95.9                         | 34.2<br>2.9  | 0.69                               | 11.79 |                                             |  | 12                       |
| <i>Ancylus fluviatilis</i>                  | Llyn Nantle                          | 23.4.70 | 29.5<br>75.2                         | 53.7<br>1.0  | 0.39                               | 53.7  | 16.8% Diatoms                               |  | 46                       |
| <i>Ancylus fluviatilis</i>                  | Tannyrallt Stream                    | 26.4.70 | 16.7<br>63.4                         | 83.3<br>36.6 | 0.26                               | 2.28  |                                             |  | 6                        |
| <i>Ancylus fluviatilis</i>                  | Upper tributary of Tannyrallt Stream | 26.4.70 | 35.0<br>57.4                         | 65.0<br>42.6 | 0.61                               | 1.53  |                                             |  | 14                       |
| <i>Ancylus fluviatilis</i>                  | R. Lowther below Reservoir           | 23.6.70 | 62.2<br>92.6                         | 37.4<br>5.0  | 0.67                               | 7.48  | 0.4% Unicellular Chlorophytes               |  | 23                       |
| <i>Lymnaea stagnalis</i>                    | Shropshire Union Canal               | 7.4.70  | 43.3<br>58.3                         | 50.0<br>43.4 | 0.74                               | 1.15  | 6.7% Diatoms                                |  | 3                        |
| <i>Lymnaea stagnalis</i>                    | Wirral Pond                          | 8.7.70  | 53.3<br>86.1                         | 43.9<br>8.6  | 0.62                               | 5.10  | 2.8% Animal remains                         |  | 18                       |
| <i>Lymnaea peregra</i>                      | Lake Dwythwch                        | 14.4.70 | 0<br>50.0                            | 100<br>42.0  | 0                                  | 2.38  |                                             |  | 3                        |
| <i>Lymnaea peregra</i>                      | Birkenhead Park Pond                 | 29.6.70 | 45.2<br>77.1                         | 54.8<br>00.4 | 0.59                               | 137.0 |                                             |  | 23                       |
| <i>Lymnaea peregra</i>                      | Shropshire Union Canal               | 7.4.70  | 34.1<br>50.0                         | 48.7<br>31.6 | 0.68                               | 1.54  | 17.2% Diatoms                               |  | 27                       |
| <i>Lymnaea peregra</i>                      | Llyn Nantle                          | 23.4.70 | 50.0<br>50.0                         | 33.3<br>50.0 | 1.0                                | 0.67  | 16.7% Diatoms                               |  | 3                        |
| <i>Lymnaea peregra</i>                      | Wirral Pond 5                        | 20.2.70 | 15.0<br>95.0                         | 85.0<br>5.0  | 0.16                               | 17.0  |                                             |  | 2                        |
| <i>Lymnaea peregra</i>                      | Wirral Pond 29                       | 5.2.70  | 46.6<br>93.1                         | 53.4<br>6.6  | 0.50                               | 8.09  |                                             |  | 47                       |
| <i>Lymnaea peregra</i>                      | Wirral Pond 1                        | 3.7.70  | 40.3<br>89.7                         | 59.7<br>0.5  | 0.45                               | 119.4 |                                             |  | 16                       |
| <i>Lymnaea peregra</i>                      | Grand Union Canal                    | 19.4.70 | 7.5<br>45.0                          | 73.0<br>4.0  | 0.17                               | 18.25 | 19.5% Diatoms                               |  | 10                       |



TABLE 3—continued

| Species                     | Locality               | Date    | + Percentage compositions in stomach |              | Concentration quotients in stomach |      | Percentage compositions of other catagories | No. of stomachs examined |
|-----------------------------|------------------------|---------|--------------------------------------|--------------|------------------------------------|------|---------------------------------------------|--------------------------|
|                             |                        |         | O.D.                                 | S.G.         | O.D.                               | S.G. |                                             |                          |
| <i>Lymnaea peregra</i>      | Wirral Pond E2         | 20.2.70 | 56.2<br>98.8                         | 43.8<br>1.2  | 0.57                               | 36.5 |                                             | 13                       |
| <i>Lymnaea peregra</i>      | Ditch at Formby Bypass | 8.5.70  | 19.3<br>57.4                         | 80.7<br>42.0 | 0.34                               | 1.92 |                                             | 15                       |
| <i>Lymnaea peregra</i>      | Wirral Pond 1          | 28.1.70 | 52.2<br>70.0                         | 44.5<br>19.8 | 0.75                               | 2.25 | 3.3% Diatoms                                | 38                       |
| <i>Lymnaea peregra</i>      | Wirral Pond 29         | 5.2.70  | 42.7<br>93.1                         | 57.3<br>6.6  | 0.46                               | 8.68 |                                             | 22                       |
| <i>Lymnaea auricularia</i>  | Grand Union Canal      | 19.4.70 | 26.4<br>50.4                         | 49.8<br>23.4 | 0.52                               | 2.13 | 23.8% Diatoms                               | 25                       |
| <i>Lymnaea palustris</i>    | Fender Valley Pond     | 11.4.70 | 55.2<br>83.4                         | 22.4<br>0.5  | 0.66                               | 44.8 | 22.4% Unicellular Chlorophytes              | 25                       |
| <i>Lymnaea palustris</i>    | Wirral Pond 1          | 3.7.70  | 30.0<br>47.5                         | 60.0<br>52.5 | 0.63                               | 1.14 |                                             | 3                        |
| <i>Planorbarius corneus</i> | Wirral Pond 9          | 8.7.70  | 44.3<br>88.8                         | 55.7<br>21.2 | 0.50                               | 2.63 |                                             | 23                       |
| <i>Planorbarius corneus</i> | Shropshire Union Canal | 10.8.70 | 40.0<br>72.5                         | 60.0<br>12.5 | 0.55                               | 4.8  |                                             | 2                        |
| <i>Planorbarius corneus</i> | Wirral Pond 13         | 3.7.70  | 76.1<br>93.8                         | 23.9<br>2.4  | 0.81                               | 9.96 |                                             | 9                        |
| <i>Planorbis carinatus</i>  | Shropshire Union Canal | 10.8.70 | 53.3<br>75.8                         | 46.7<br>17.5 | 0.70                               | 2.67 |                                             | 6                        |

+ Where  $\frac{\% \text{ Conc. Stomach}}{\% \text{ Conc. Intestine}} = \text{Conc. Quotient for stomach.}$



differences in diets for a given water body. This is probably a reflection of different niches and microhabitats for the different species. For example, in the River Lowther *Ancylus fluviatilis* feeds on the underside of stones, whereas *L. peregra* feeds on the top of the same stones and is the only snail which ingests filamentous algae. Also, in the Shropshire Union Canal *V. viviparus*, which was confined to sediments during the sampling time, contained very few diatoms, whereas all those other species found on concrete walls and marginal macrophytes were full of diatoms. Thus I feel that diet availability is being reflected, not diet selection. The absence of large macrophytic fragments and animal remains from both the smallest species, and smaller size classes among all species, indicates that the mouth diameter is too small to allow either to be ingested.

## DISCUSSION

The present author and numerous others found a wide range of diet items, including living algae, bacteria, detritus, animal matter and sand grains. Frömming (1956) stressed the effect of a varied and balanced diet on increasing growth rate of *P. corneus*, for example. Pure diets have also been used in rearing snails. Rodina (1948) reared *B. tentaculata* on bacteria, Tsikhon-Lukanina (1958, cited in Gaevskaja, 1966) reared *L. peregra ovata* on macrophytes and Xavier, Azevedo and Avalino (1968) reared *Bulinus contortus* for 2 generations on the blue-green alga, *Oscillatoria formosa*.

Bequaert (1928, cited in Frömming, 1956), mentioned that *Lymnaea* species are occasionally carnivorous, and Bovbjerg (1968) found that four American herbivorous species of the same genus required some animal food. Although the author found animal remains such as protozoans, rotifers, nematodes, polyzoan statoblasts, oligochaete chaetae, microcrustacea and insect appendages, in the guts they were most numerous in the larger pulmonates and absent from the prosobranchs. They may have been accidentally ingested in the periphyton and sediments when dead or trapped.

Frömming (1956) and Gaevskaja (1966) stated that most pulmonates ate fresh macrophyte tissue, the latter author cited Tsikhon-Lukanina who found they formed the bulk of food intake in 200 *L. stagnalis*, although decaying plant fragments were more frequent than fresh fragments. Calow (1970) analysed 100 *L. peregra* and found very little macrophyte ingestion, but a predominance of periphytonic algae on leaves of *Elodea canadensis*. This author found more macrophytic fragments in the larger weed dwelling pulmonates and benthic prosobranchs but no species ingested more than 1% by diet composition. Lang (1968) found the chief diet of the North American stream dwelling prosobranch, *Goniobasis proxima*, was dead tree leaves.

Numerous authors, including Frömming (1956), stressed the presence of detritus in the guts of water snails. This author found it formed the major diet component by percentage composition and frequency of occurrence in all twenty species. This suggests four possibilities:

1. Digestion and assimilation of detritus.
2. Digestion and assimilation of associated bacteria and fungi.
3. Digestion and assimilation of both detritus and its microflora.
4. Digestion and assimilation of neither detritus nor its microflora.

Until the recent work of Calow (1973 and 1974), diet selectivity was not critically tested. Schmid (1932, cited in Frömming, 1956) thought that *A. fluviatilis* preferred submerged lichens, Boycott (1936) that *L. peregra* may be selective for algal species and Standen (1951) and Wright (1960) that juveniles showed optimal growth on green algae, with a diet change in the adults. Gaevskaja (1966), reviewing Russian work, gave laboratory evidence for macrophyte preference and refusal by fourteen species of *Elodea canadensis*. Frömming (1956) showed that *L.*



*stagnalis* rejected this species of water plant, and the present author confirmed this, with *V. viviparus*, *B. tentaculata*, *L. peregra*, *G. albus* and *P. fontinalis*. Calow (1970) found *L. peregra ovata* rejected the same water plant and, by using feeding experiments, suggested that greater liver string production on filamentous green algae rather than on diatom diets, indicated a preference for the former.

Calow (1973a, b) found that in Malham Tarn the stone dwelling *A. fluviatilis* preferred diatoms, especially *Gomphonema*, whereas stone dwelling *B. contortus* ingested bacteria. Using a field and laboratory approach in 1973 he found that *A. fluviatilis* showed the following preference order: algae > lichens > detritus > fungi, whereas *B. contortus* preferred detritus > algae > fungi. This author found that algae are less frequent in the guts of *A. fluviatilis* than detritus, but more so than fungi. Also diatoms form the most frequent algal diet. Laboratory feeding trials showed that juvenile *V. viviparus* and *G. albus* rejected the filamentous green alga *Oedogonium* and the filamentous xanthophyte *Vaucheria*. *B. tentaculata* may prefer the unicellular green algae *Chlorella*, *Ankistrodesmus* and *Scenedesmus* over the filamentous algae *Oscillatoria*, *Oedogonium* and *Vaucheria*.

Much published work is confusing. For example, Frömming (1956) says that *L. stagnalis* rejected the macrophyte *Ceratophyllum demersum*, whereas Gaevskaja (1966) says it is selected by that species of snail. This is one of numerous examples illustrating the lack of critical experimental research into snail diets.

Another problem is the question of locating the food source. Are snails indiscriminate feeders, or do they move towards diets? Bovbjerg (1968) found that *Stagnicola reflexa* made continuous random movements until it chanced upon a suitable diet. He showed there was positive chemotactic movement towards chopped crayfish, as did Clampitt (1970) using individuals of two species of *Physa*. Calow (1973a), during both field and laboratory experiments on *A. fluviatilis* and *B. contortus*, suggested that food seeking was random with contact chemoreception. The present author found no evidence of chemotactic response by *G. albus* to algal food.

Frömming (1956) said that snails are inefficient feeders as they spend most of their moving time in feeding activities. Grime, Dearman and McPhearson-Stewart (1968) found that land snails had inefficient digestive processes as most of their food passed through without alteration in appearance, and this is confirmed by the author for the freshwater snails. Assimilation efficiencies taken from various authors range between 4 and 40% in freshwater snails feeding on detritus.

I found that *Planorbarius corneus* had a higher growth rate on eutrophic than on oligotrophic detritus, which may reflect the greater nutritional potential of the former. Probably eutrophic detritus contains both more bacteria and a different species composition than oligotrophic detritus. They probably correspond respectively to Rodina's (1966) juvenile and senescent detritus types. She found higher total bacterial numbers in juvenile than senescent detritus. This probably confirms the fact that eutrophic detritus has a higher nutritional potential than oligotrophic detritus.

Carriker (1945) established the necessity for sand grains in the diet. Storey (1970) found them in the guts of 100 *L. peregra*, and that they occupied most of the gizzard, crop and pylorus. Although Storey's replicates were too small to be significant, he showed that the addition of sand grains to the diet of *Lymnaea peregra* resulted in an increased growth rate, presumably as a result of their grinding action in food digestion. This author found no sand grains in the following species: *V. piscinalis*, *B. tentaculata*, *A. vortex*, *G. albus*, *A. crista*, *V. viviparus*, *P. fontinalis* and that they occurred in the following species: *P. jenkinsi*, *P. corneus*, *H. complanatus*, *A. hypnorum*, *P. carinatus* and *L. palustris*. The highest concentration occurred in the lymnaeids: *L. truncatula*, *L. peregra*, *L. auricularia* and 15% by composition in *L. stagnalis*.

One of the unsolved problems in aquatic gastropod ecology is what factors regulate the distribution of a given population. Geyer (1909, cited in Frömming, 1956) stated that an



increased size of water body gave an increased nutritional potential by increasing the range of available habitats and thus diets. Also increased water movement, environmental stability and plant build up were optimal. Boycott (1936) stated that an optimal habitat for aquatic molluscs included water with a large surface area, slow flowing, warm, clear and fairly hard with good macrophyte growth. He grouped snails into hard water ( $> 20$  mg/l calcium ions), soft water ( $< 20$  mg/l calcium ions) and calcium indifferent species.

Numerous subsequent authors have stressed the importance of calcium as an essential element for shell formation. Frömming (1956) said from his experimental evidence, that the required calcium level is provided from the macrophyte diet, but his experimental procedure was uncritical. Klein and Traut (1961) found radioactive calcium taken from the water by the freshwater prosobranch *Melanoides tuberculata*, van der Borgh and Puymbroeck (1966) showed 80% was taken up from water, and only 20% from the food. Harrison and Shiff (1966) from Rhodesian work, said species in low calcium waters were smaller in adult size and showed lower population densities. Alves (1958) also from Rhodesian work, said that snail vectors of schistosomiasis preferred higher calcium levels. Boettger (1944) said calcium deficiency was the primary limiting factor. However, Hilbert (cited in Frömming, 1956) found *L. palustris* with thick shells in calcium deficient moorland water. Also, Young (1975) reared a range of species, including so called calciphiles, from egg to egg in cages suspended in a 4 mg/l calcium concentration mountain lake. He also reared them in calcium-poor and calcium-rich water on a lettuce diet in the laboratory. His  $^{45}\text{Ca}$  experiments suggested that *L. peregra* and *P. corneus* took up calcium from both food and water. Hubendick (1957) remarked that species distributions were regulated by the interactions of several factors. Fretter and Graham (1962) said the increased prosobranch diversity in harder waters was due to an increase in macrophyte crops, which provided more shelter and increased detritus production. Hubendick (1957) said snails have undifferentiated diets, and that nutritional problems were due to chemical conditions hindering food utilization. Gaschott (1928, cited in Frömming, 1956) pointed out that populations of *Valvata geyeri* from oligotrophic waters were dwarfed compared to those from eutrophic waters. Are we seeing the effects of nutritional potential of the two types of detritus? Abdel Malek (1958) said that population densities were directly correlated with diet quantity not quality, although Eisenberg (1966), in a critical experimental study, showed that the population density of *Lymnaea elodes* was limited by food quality rather than quantity. The density was regulated through negative feedback by adult fecundity. The same author (1970) said that intraspecific competition for enough food to reproduce is the limiting factor. Perhaps different species have different assimilation efficiencies on detritus and other diets?

Finally I would like to suggest very tentatively that both diet quality and quantity may regulate species distributions, and that the detritus diet assimilation efficiency (the amount which is actually digested and used) depends on the amount and kind of bacterial flora associated with it, and that British aquatic snails are directly regulated by food requirements rather than by calcium concentrations. As detritus forms the major diet of all twenty species examined, possibly Boycott's so called calcifuges can reproduce on dystrophic or oligotrophic detritus with a lower nutritional value, but cannot compete with calciphile species on eutrophic detritus.

Macan (1963) discussed the correlation of environmental factors with freshwater invertebrate distribution, and decried the lack of experimental work. Thus, I hope that this elementary paper may well stimulate much more intensive and critical studies at the ecophysiological and biochemical level, in relation to field observations, such as the recent scholarly work by Calow (1970, 1973a, b, 1974) and Mason (1970).

#### SUMMARY

Dissection of 1,300 aquatic gastropods using 20 species from 24 different sites, showed that



detritus formed from 50-90% of the gut contents by volume. This underlines the importance of detritus compared to other items of diet. For example, algae never exceeded 10% by volume, with diatoms and unicellular Chlorophyta forming the dominant algal groups. Fresh macrophyte fragments were rare, even in the larger pulmonates (*L. stagnalis*, *L. palustris* and *P. corneus*). This is in complete disagreement with Gaevskaja (1966) who cites Tsikhon-Lukanina (1958, 1961) as finding the guts of 3 species of *Lymnaea* filled mostly by macrophyte fragments, although decaying macrophytes were consumed more than fresh ones. Gaevskaja also noted that *L. stagnalis* damaged macrophyte beds. This author found that macrophytes were not important in freshwater gastropod diets, although until critical experimental designs are operated under natural field conditions, it is not possible to draw definite conclusions.

Thus in the author's opinion, the aquatic gastropods examined by him are rarely primary consumers feeding on living plants, but are detritivores living on dead or decaying matter. Laboratory experiments showed no evidence for positive chemotaxis towards plant diets or for any diet selection. However the fresh-growing macrophyte, *Lemna trisulca*, was selected by four out of six species of snails. Frömming (1956) and Gaevskaja (1966) both confirmed selective feeding on macrophytes.

Most species ingested a varied diet of detritus, algae, decayed macrophytic fragments, and animal remains. In the laboratory maximal growth rates occurred on a balanced diet. The only evidence of a seasonal change of diet was the midsummer increase in animal remains, possibly due to an increased availability of dead invertebrates during the warmer season.

#### ACKNOWLEDGEMENTS

This paper is a shortened version of a thesis presented as a topic for part requirement for the degree of M.Sc. in Freshwater Biology at Liverpool University.

I wish to thank the National Environmental Research Council for receipt of a grant, without which this work would have not been possible. Thanks are given to my Supervisor Dr. J. O. Young for suggesting the topic, and to Dr. E. White, Dr. J. Eaton and Dr. T. Gray for discussions. I am deeply indebted to my wife for translating much of Frömming's book and various German papers. I thank Mr. B. Djakov for translating Rodina's paper from the Russian. For permission to work in the Botany department of Liverpool University, I thank Dr. T. Gray. Mrs. L. Bisschoff of Zululand University typed the manuscript. Also I wish to thank Mr. J. Gittings for assistance with the field work. Finally, I wish to thank Mrs. N. F. McMillan for encouraging me to publish and her continued interest in the work.

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## REVIEWS

*Pathways in Malacology*. Edited by S. van der Spoel, A. C. van Bruggen and J. Lever. Bohn, Scheltema & Holkema, Utrecht. dr. W. Junk b. v., Publishers, The Hague. 1979. ISBN 9031303194, 295 pp. Price US \$72.

As one who was unable to attend the sixth international congress of Unitas Malacologica Europaea, held in Amsterdam in 1977, it was with keen anticipation that I received this book for review. It comprises eleven chapters, each devoted to one of the invited lectures given at the congress. These are essentially review papers and the subjects covered are extremely wide ranging. Clearly each reader will follow his own particular specialist interests; mine led me to Solem's characteristically thought-provoking chapter on the historical biogeography of land snails and to Joosse's excellent survey of the complex hormonal systems found in molluscs.

A number of the chapters are self-recommending, and whilst some others have less obvious general appeal, all are rewarding. Sir Maurice Yonge's review of cementation in the Bivalvia and Wells' elegantly written account of octopus behaviour, for example, must be considered essential reading. Also of general interest are reviews of torsion by Lever and of deep-sea bivalves by Knudsen. The remaining, more specialist subjects to be covered are embryonic symmetry, shell formation, energy metabolism, pest control, and planktonic molluscs.

The editors have done an outstanding job in maintaining a high standard of presentation throughout this book, especially as English is not the native tongue of many of the authors. The book is also beautifully produced but sadly this seems to have raised its price well beyond the pockets of most private purchasers. However, this is the sort of book to which anyone interested in molluscs should have access, and it ought to be on the shelves of all major scientific libraries.

PETER B. MORDAN

*A magyarországi recens puhatestűek elterjedése.* [Distribution of the recent Mollusca of Hungary.] By L. Pintér, A. Richnovszky and A. S. Szigethy. *Soosiana*, Supplement I. Budapest, 1979. VI, 351 pp., 222 distribution maps. ISSN 0133-7971.

This is the first grid-square distribution atlas for the non-marine Mollusca of an entire country, apart from the British Isles. It is a remarkable achievement, even though Hungary is a relatively small country (less than one-third the area of the British Isles) and that coverage is still very imperfect. The bulk of the data was collected in less than five years, about 50,000 records being incorporated. In the authors' words: '... every Hungarian malacologist possessing [his] own collections joined into the mapping project and the data ... were at our disposal.' The organization of the scheme was comparable to that in Britain, involving the use of printed record cards and adopting the 10-kilometre square (1025 in Hungary) as a basic mapping unit. Three classes of records are shown on the maps: post-1950, pre-1950 only, and shells from the flood rubbish of rivers. Eight species are represented solely by the last category. It is interesting to note that many of the maps reflect a bias of a kind met with in the early stages of all such schemes: the picturesque mountain areas in the north of the country have proved attractive to conchologists, whilst the dull stretches of the Hungarian plain remain poorly explored. The provisional nature of the maps is fully accepted by the authors. 'All the attainable records of recent Hungarian Mollusca have been collected ... The summing up revealed the shortcomings and the insufficiency of the records, and ... we have to aspire deliberately to explore the blank spots.'

The book is organized as follows: an introduction, in Hungarian, English, French, German and Russian (pp. 1-40); the distribution maps, two per page (pp. 41-153); a catalogue of the species with lists of localities and habitats within each 10-km grid square (pp. 154-341); a glossary of habitat terms, translated into five languages (pp. 342-345); and an index. Some additional gridded records are published in *Soosiana* 7 (1979), pp. 97-108.

M. P. KERNEY



**THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND**

**INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31st DECEMBER, 1979**

| Publications:                                | £   | £         | Fees and Subscriptions:                         | £   | £         |
|----------------------------------------------|-----|-----------|-------------------------------------------------|-----|-----------|
| News Letter . . . . .                        | ... | 1,383.58  | Membership Fees . . . . .                       | ... | 2,524.40  |
| Student Papers . . . . .                     | ... | 148.43    | Subscriptions . . . . .                         | ... | 1,224.17  |
|                                              |     |           | Entrance Fees . . . . .                         | ... | 25.00     |
| Journal:                                     |     |           |                                                 |     | 3,773.57  |
| Volume 30 No. 1 . . . . .                    | ... | 1,987.03  | Grant from Royal Society . . . . .              | ... | 1,000.00  |
| Volume 30 No. 2 . . . . .                    | ... | 1,879.45  | Donations . . . . .                             | ... | 184.56    |
| Covers for Volume 30 . . . . .               | ... | 285.82    |                                                 |     |           |
|                                              |     |           | Sales:                                          |     |           |
|                                              |     | 4,152.30  | Atlas . . . . .                                 | ... | 84.40     |
| Cost of Atlas, Postage and Packing . . . . . | ... | 24.99     | Advertising . . . . .                           | ... | 2.00      |
| Printing, Stationery and Postage . . . . .   | ... | 751.11    | Journals . . . . .                              | ... | 127.62    |
| Officers Expenses . . . . .                  | ... | 215.22    | Student Papers . . . . .                        | ... | 74.60     |
| Subscriptions . . . . .                      | ... | 14.00     | News Letter . . . . .                           | ... | 4.25      |
| Meetings . . . . .                           | ... | 50.00     | Sundries . . . . .                              | ... | 4.60      |
|                                              |     |           |                                                 |     | 297.47    |
|                                              |     |           | Investment Income:                              |     |           |
|                                              |     |           | General Account . . . . .                       | ... | 1,077.58  |
|                                              |     |           | Life Members Fund . . . . .                     | ... | 325.07    |
|                                              |     |           | Reserve and Research Fund . . . . .             | ... | 156.23    |
|                                              |     |           |                                                 |     | 1,558.88  |
|                                              |     |           | Transfer to Reserve and Research Fund . . . . . |     | 156.23    |
|                                              |     |           |                                                 |     | 1,402.65  |
|                                              |     | 6,739.63  |                                                 |     | 6,658.25  |
| Net Surplus . . . . .                        | ... | —         | Net Deficit . . . . .                           | ... | 81.38     |
|                                              |     | £6,739.63 |                                                 |     | £6,739.63 |







# PROCEEDINGS OF THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

## TREASURER'S REPORT, 1979

As predicted in my report for 1978, the accounts for 1979 show a deficit.

Our total income from all sources is very much the same as that for 1978, excluding a grant of £1,000 for which we are grateful to the Royal Society. This grant was made towards the cost of publishing a Special Paper, which is at present in the press.

Unfortunately expenditure has mounted sharply, since printing and postal charges are both very much higher; it appears inevitable that this trend will continue.

The Annual Subscription rates for Members and the *Journal* subscription rates for non-Members have been increased from 1st January, 1980, and it is hoped that the increased income will meet foreseeable expenditure. Members are urged to send their subscriptions promptly without reminders, since these are now expensive. Your Council will continue to administer the affairs of the Society with maximum economy.

29 Members and 5 Junior Members are in arrears with 1979 subscriptions. All Members should note that no further publications will be sent in 1980 to those whose current subscriptions remain unpaid, although any publications which have been withheld will be sent on payment of arrears.

MARJORIE FOGAN

*Hon. Treasurer.*

## REPORT OF THE COUNCIL 1979-1980

*Membership.* It is with regret that the Society has to report the deaths of the following members:— Brigadier E. A. Glennie, who joined the Society in 1950 and died on 15 February, 1980 after a long illness, and F. Mayer, who joined the Society in 1962. Membership now stands at 607, comprised of the following categories:— Full members 537 (34 life members); Family members 42 (8 family members); Honorary members 4; Junior members 22. During the year 25 members resigned, 20 were struck off for non payment of subscriptions. 61 new members were elected.

*Subscribers.* The total number of subscriptions now stands at 170. During the year there were 7 cancellations and 4 new subscriptions.

*Meetings.* Seven ordinary meetings were held during the year in the British Museum, Natural History, as well as one annual general meeting and a special general meeting.

*Field meetings.* Seven field meetings were held during 1979 as follows:— 14 April, Bramerton, Norfolk; 25 May, joint meeting with the Yorkshire Conchological Society; 24 June, joint meeting with the Northampton N.H.S.; 21 July, Sandwich, Kent; 22 September, Peterborough, Northants; 6 October, Cornard Mere, Suffolk; 21 October, joint meeting with the Basildon, N.H.S. Thanks are due to the following for leading these meetings:— Mrs. C. J. Pain, Messrs. P. Cambridge, I. M. Evans, A. Norris, J. Llewellyn-Jones, A. G. H. Osborn and E. Milne-Redhead.

*Publications.* Two parts of the *Journal of Conchology*, volume 30 parts 1 and 2, and four quarterly *Conchologists' Newsletters* were issued. Paper for students no. 17, *An introduction to the Scaphopoda*, was issued in May, 1979.

## RECORDER'S REPORT: NON-MARINE MOLLUSCA

Interest in grid mapping continues, both at a national and a local level. The first tetrad ( $2 \times 2$  km square) atlas, compiled by Dr. Preece for the snails of the Isle of Wight, is expected to appear in April, 1980 (Sandown Museum special publication). A revised set of Irish maps is being prepared, for publication by the Ulster Museum as part of a catalogue of the Irish non-marine molluscs in their collections.

The following vice-county novelties have been verified since the last Report (*J. Conch.*, *Lond.* **30**, p. 143). In all cases the date of collection was 1979-80. It should be noted that vice-comital records of a number of recently segregated but



evidently widespread species (e.g. of *Arion*) are not normally published in these Annual Reports, though I will gladly send current information about the distribution of any of them on request.

Cornwall West (1): *Lymnaea stagnalis*, Phillack (10/5639), J. Humphreys.

Devon North (4): *Lymnaea stagnalis*, Braunton (21/4835), Miss M. Jaques.

Sussex East (14): *Boettgerilla pallens*, Horsted Keynes (51/3528), B. Colville.

Bucks (24): *Pyramidula rupestris*, Weston Underwood (42/8651), A. G. Osborn.

Norfolk East (27): *Boettgerilla pallens*, Wymondham (garden, 62/0996), Miss M. M. Elliott.

Norfolk West (28): *Milax gagates*, Wells-next-the-sea (53/9243), M. J. Bishop.

Warwick (38): *Pisidium tenuilineatum*, R. Avon, Stratford (42/1853), D. H. Keen.

Brecon (42): *Limax pseudoflavus*, Hay-on-Wye (32/2342), S. P. Dance.

Lancaster West (60): *Pisidium supinum*, *P. moitessierianum*, Carnforth (canal, 34/4969), Mrs. M. Fogan.

York Mid-West (64): *Boettgerilla pallens*, Leeds (garden, 44/2637), B. Colville.

Durham (66): *Vertigo genesii*, Widdybank Fell, Middleton in Teesdale (35/8230), B. Colville and B. Coles.

Haddington (82): *Hydrobia ventrosa*, West Barns, Dunbar (36/6678), T. Warwick; *Deroceras agreste*, Broadsands (36/5285), A. T. Sumner.

Edinburgh (83): *Deroceras agreste*, Harperrig reservoir (36/0860), A. T. Sumner.

Fife (85): *Oxychilus helveticus*, Inverkeithing (36/1383), A. T. Sumner.

South Ebudes (102): *Limax pseudoflavus*, Port Charlotte, Islay (16/2558), Dr. Shelagh Smith.

North Ebudes (104): *Lymnaea palustris*, *Vertigo antiverigo*, *Acanthinula aculeata*, Lock Cill Chriosd, Skye (18/6120), M. J. Willing.

Caithness (109): *Arion lusitanicus*, Thurso (39/1068), R. G. Meiklejohn.

Donegal East (H 34): *Vertigo angustior*, Ballycramsy (24/4351); *Ashfordia granulata*, Kinnagoe Bay (24/6245), both R. Anderson.

Donegal West (H 35): *Pyramidula rupestris*, Heelin Port (13/7170); *Ashfordia granulata*, Downings (24/1038), both R. Anderson.

The outstanding discovery of 1979 is *Vertigo genesii* in Teesdale. This species has an arctic-alpine distribution, being found in the mountains of northern Scandinavia and in the Alps. Though it is common as a fossil in Late-glacial deposits in Britain, it has hitherto been thought extinct here. Its survival in Teesdale is nevertheless entirely in keeping with the well-known occurrence of many glacial relict plants in the same area.

Also worth noting is the discovery of a colony of living *Vertigo angustior* in a damp grassy dune pasture in Co. Donegal. This rare snail is usually collected only as dead shells and it must certainly be regarded as an endangered species in the British Isles.

M. P. KERNEY

## RECORDER'S REPORT: MARINE MOLLUSCA

Twelve area representatives attended a meeting at South Shields Museum on 2 June, 1979, hosted by Mr. F. R. Woodward, the Principal Keeper of Natural Science. Aspects of the marine census were discussed in a lively meeting and support was obtained for the preparation and publication of species lists for all sea areas. Dr. Roger Mitchell of the Nature Conservancy Council agreed that N.C.C. would publish these and copies of *Marine Mollusca of Britain and Ireland* were distributed to area representatives in February, 1980. A few copies are still available from Dr. R. Mitchell, Nature Conservancy Council, Godwin House, George St., Huntingdon, PE18 6BU.

I am now using these lists to draw up distribution maps of all the species on a sea area basis and N.C.C./B.R.C. have agreed to publish these as an interim atlas about the end of 1980. This is another step on the way to publication of a more detailed atlas, hopefully about three years later.

Meanwhile, a most important regional contribution to the knowledge of marine molluscan distribution has appeared in the form of *Marine Mollusca of East Scotland*, by D. W. McKay and Dr. Shelagh Smith (both area representatives for the marine census), which has some 413 hand drawn maps. Although not connected with the Society's scheme, nevertheless this atlas does show what can be produced on a regional basis by representatives cooperating and may perhaps be emulated by others to provide detailed localized mapping, impractical on a larger national or international scale.

Several changes have occurred in the list of area representatives and this will now form an appendix to the list of members published with the Newsletter in July.

D. R. SEAWARD



## INSTRUCTIONS TO AUTHORS

Authors of papers submitted for publication in the *Journal of Conchology* are urged to pay careful attention to the following notes. Any author who has difficulty in complying with these requests, or has queries concerning manuscripts, should consult the Hon. Editor **before** submitting a manuscript.

1. Manuscripts should be sent to the Publications Committee, c/o Dr. M. P. Kerney, Dept. of Geology, Imperial College, London SW7 2AZ.

2. **Two** copies of all text and illustrations should be submitted. (A few years ago the entire copy for one issue of the *Journal* was lost in a mail robbery!). Authors are strongly recommended to retain a further copy for proof correction.

3. The text should be **fully revised**, typed **double spaced** with wide margins (at least 1 inch), pages numbered consecutively and should conform in style to recent issues of the *Journal*. Titles should be concise and apposite, address(es) of author(s) should follow the title. Linear measures and weights should be metric and authorities for specific names should be given when first mentioned. Location of voucher material should be stated wherever possible. A brief, but informative, abstract should precede the main text.

4. Originals of text-figures should be  $1\frac{1}{2}$ –2 times the final size but should not exceed 25 by 36 cm. They should be drawn in Indian ink on clean ground, numbers consecutively, and referred to in the text as “Fig. 1”, etc. Authors are strongly urged to construct text-figures so as to make full use of the page width and to submit a copy reduced to final (published) size wherever possible. Lettering should be legible and not less than 1 mm high after reduction.

5. Plates should only be used when essential and **must** not exceed 19.5 by 15 cm. They should utilise quality prints showing fine detail and moderate contrast. As far as possible prints on one plate should be matched for contrast and brightness. Authors are urged to make fullest use of plate space due to the high cost of printing plates. In the text the explanations of text-figures and plates should follow the references.

6. Tables should be concise, fit into the text and table headings should be self explanatory wherever possible. Tables are not printed “boxed”.

7. All papers referred to in the text (including synonymy lists) should be listed alphabetically by author's surnames at the end of the text under “References”. For books give author's name, initials, date, full title, pages, plates and place of publication.

*e.g.*

ELLIS, A. E. 1926. *British snails. A guide to the non-marine Gastropoda of Great Britain and Ireland, Pliocene to Recent*. 275 pp., 14 pls., Oxford.

BROWN, P. and STRATTON, G. B. (Editors). 1965. *World list of scientific periodicals published in the years 1900–1960* (4th Ed.) 3 vols. London.

For periodicals give full title of the article, title of the periodical abbreviated according to the World List (4th Ed.), volume number, page numbers and plates.

*e.g.*

WOODWARD, F. R. 1965. Monograph of the British Lower Tertiary Unionidae, with descriptions of three new species. *J. Conch., Lond.* **25**: 316–330, pls. 22–27.

GOULD, S. J. 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail. *P. (Poecilozonites)* in Bermuda. *Bull. Mus. comp. Zool. Harv.* **138**: 407–532, 5 pls.

8. Authors may obtain copies of all papers at cost price if ordered from the printers, via the Hon. Editor, when the galley proofs are returned.



# Journal of Conchology

Vol. 30, Part 4, October 1980

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Mollusks

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# SOME THOUGHTS ABOUT *MARMORANA* HARTMANN 1844

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(Presidential address, delivered before the Society at the British Museum, Natural History, 15 March, 1980)

## INTRODUCTION

Over the years my thoughts on *Marmorana* have changed and may change again. Hence the vague title. However *Marmorana* is largely a genus of Italian snails included in subfamily Helicinae. There are four subgenera; *Murella* mostly from Sicily; *Ambigua* from the mainland, southeast of Tuscany; *Tyrrheniberus* from a narrow enclave in the middle of the east coast of Sardinia; and of course, *Marmorana* itself on which I shall be concentrating. My present thought is that this consists of one species only, *serpentina* (Férussac) with many forms. Pilsbury in Tryon (1888-1894) describes some of these but that seems to be the latest, if not the only, work in English.

Few of the earlier authors visited Sardinia or Corsica and saw the specimens alive in their habitats. They did not realise the great variability even within one locality. Their definitions were often based on the few specimens supplied by other travellers who may have been botanists, geologists, archaeologists, or just tourists but were seldom malacologists and, it seems, did not know the need for accurate localities. On the latter point I think that the localities recorded as 'near Ajaccio' and 'near Sassari' have to be given a tolerance of up to 150 km.

The result is that later authors dispute what, if anything, is represented by a particular illustration and contradict each other as to the presence or absence of a particular form at a defined locality. One reports true *serpentina* from Sardinia; another denies it. Form *hospitans* from Cagliari is also reported from Bonifacio in Corsica; this is denied by a second author and a third, while denying it, admits at Bonifacio a form so close to *hospitans* that he calls it *pseudo-hospitans* of which more later.

To clear the way I will mention first two species or forms than may not be *serpentina* or even *Marmorana s.s.* In 1894 R. Meli reported on specimens of *Ambigua signata* (Férussac) which he had found on Monte Circeo, a rocky limestone outcrop on the Italian coast midway between Rome and Naples. Kobelt went there in about 1902 and in Rossmässler (Neue Folge, vol. 10, p. 62-63) describes species *melii*, based on one specimen, and the less rare *circeja*. He treats them as *Marmorana s.s.* The one now disintegrated dart that I obtained from *circeja*, I think, supported this, but the shells look so like *Ambigua signata* which is abundant on the Monti Ausoni just inland, that Meli may have been right. Now for *serpentina*.

*Marmorana serpentina* form *serpentina* Férussac 1821.

Férussac described *serpentina* in 1821. Just 15 years later Rossmässler himself (vol. I, part iv p. 9) after a description - not quite Férussac's - says; 'Varieties. These are almost as many as the places where they are found'. More have been described, pretty indifferently, since then. I shall not try to give descriptions now, but propose to view the forms as possible local races within



definable areas. However, Férussac's 1821 description was:— 'Helix. Shell depressed orbiculate; subperforate; rather thin and smooth; whitish, banded regularly with numerous small equal reddish-brown marks; spire blunt; columella red; edge of lip subreflexed.' His illustration is excellent. I add as dimensions, diameter 18 mm, height 10 mm, and the colour of the columella seems to me to be brown.

The four subgenera of genus *Marmorana* are anatomically distinct. Of *Marmorana s.s.*, that is to say, species *serpentina*, I need only say that the slightly curved dart has a cross-section like a script  $\propto$  the four blades curving towards each other in pairs, leaving only a narrow gap between each pair of blades. The mucous glands on the vagina in the majority of specimens (K. L. Pfeiffer (1946) quotes 37 out of 52) each fork into two branches. There and in other organs, there is a tendency to irregular minor variations, of doubtful value when only two or three specimens have been examined.

It is assumed that *serpentina* originated in Sardinia or Corsica, landing by ship at Leghorn where Férussac found it, and at Viareggio, on the coast of Tuscany and spreading inland up the Arno valley to Pisa and Lucca and thence to Siena and Florence. It seems to cling to man-made localities, walls *etc.* At San Giuliano Terme near Lucca it is found on walls and trees near the Bathing Establishment, but shuns the limestone cliffs above the town. K. L. Pfeiffer comments that his specimens from the harbour walls at Leghorn were smaller than those found earlier by Ambrosi. He explains this as perhaps due to the dust from motor traffic making the walls less desirable habitats. The marking on the exposed upper surface of my still more recent specimens from two lorry parks there is largely erased. May this not be due to diesel fumes?

*Marmorana serpentina* form *trica* Paulucci 1882.

This is the only other mainland form and is plainly a local race of *serpentina*, differing in its rather higher spire and distinctive marking. It is found around Toulon in the south of France, notably at St. Cyr.

The other forms of *serpentina* are restricted to Sardinia and Corsica. Germain's works of 1929 and 1930 give a modern view of the forms found in Corsica, but I am doubtful whether some of the forms which he suggests are common to both islands, are identical. They may be only rather similar. K. L. Pfeiffer (1946) deals with his own hunting in southern Sardinia in 1935 and much work later in German museums. He hoped to visit the rest of the island later, but it seems he never did. His comments on the museum specimens from the north are however most helpful, as the position is far less clear cut there.

#### *Geology of Sardinia.*

The eastern half of the island is of granite and shales, except for the limestone of the Tyrrheniberus enclave (roughly from Baunei to Siniscola on the east coast) and two other areas, one surrounding Isili, Laconi and Seui and the other, the Tacquisara valley, from Monte Arqueri to Jerzu. To the north of the Tyrrheniberus enclave, the eastern part of Isola Tavolara and the tip of Capo Figari are also limestone. The southwestern bulge of the island is also of granite. These two granite areas are separated by the Campidano, a lower lying area of Quaternary deposits and recent alluvium and an area of Miocene marls and clays. The San Antiocho peninsula and thereabouts on the southwestern extremity is of volcanic rocks which occur isolatedly on the Campidano and the marls and clays. Volcanic rocks form most of the northwestern quarter but there is another substantial area of marls and clays widely around the northern city of Sassari. The extreme northwestern tip is mainly granite with two small areas of limestone near Alghero.

*Marmorana serpentina* form *hospitans* Bonelli in Rossmässler 1836.

In the urban area of Cagliari in the middle of the south coast of Sardinia on the edge of the marls and clays, and particularly in the Roman amphitheatre and roadside cuttings, *hospitans* is found.



It is rather larger and more globose than true *serpentina*; it is often bluntly keeled; the markings are pale on a white base. Bonelli never described it but Rossmässler (Vol. I part iv. p. 9) did so by reference to his figures 240 and 241. Cantraine (1840) was not satisfied and described it again and named it as *magnettii*. These are the same thing and the only form found at Cagliari.

*Marmorana serpentina* form *carae* Cantraine 1840.

West of Cagliari at Capoterra on the foothills of the granite and westwards thence via Monte Santo di Pula and Teulada, perhaps as far as San Antiocho, the form *carae* is found but only rarely and in ones and twos. It occurs also east of Cagliari on the granite at Campo Omu and Monte Sette Fratelli, and on my findings at Dolianova, a little to the north.

Paulucci (1882) comments that, unlike the other forms of *serpentina* which had been sent to her, which lived exposed on rock faces 'defying the sun', *carae* lives under stones like a *Campylaea*. The whorls are only slightly swollen and except the last whorl show occasional fine granulations; the well marbled upper surface has a yellowish-brown epidermis; the lip and walls of the aperture are wholly white. There is, however, a narrow yellow band at the edge of the callus on the inner wall of fresh specimens where the callus has overlaid and preserved the yellow epidermis.

On the grounds of its unusual habitat and the fact that the darts he obtained (TWO at most) were straighter than the slightly curved dart of *serpentina*, K. L. Pfeiffer (1946) described *carae* as a separate species. As I have found other forms living under stones, I am not convinced.

*Marmorana serpentina* form *isilensis* Villa in Mabilie 1867.

This is another form which the alleged author, Villa, (or it may have been one Pintor) never described. It comes from the limestone around Isili, Laconi and Šeui. The shell is rather solid, glossy and white. Many have a distinct zigzag marking but not a few remain without marking. The outstanding character is the very dark brown callus on the inner wall of the aperture. The form extends eastwards to Monte Arqueri where Pfeiffer (1946) found it in small numbers among much larger quantities of the next form, *isarae*. It is unusual for two such distinct forms to be found living together.

*Marmorana serpentina* form *isarae* Paulucci 1882.

The limestone strip west of the Tacquisara valley forms the dolomite caps on the mountain ridge from Monte Arqueri to Pizzi di Podini near Jerzu. On the caps and also on the large boulders that have fallen into the valley, form *isarae* is abundant. It is smaller than typical *serpentina*, thin, finely striate and very richly and delicately marked. Near the cave of San Giorgio near Ulassai larger specimens are found. The aperture is white except for the merest fleck of brown at the base of the columella which is seldom absent. Pfeiffer (1946) reports that of 11 specimens dissected, 7 had unbranched mucous glands, reversing the usual majority in *serpentina* of branched mucous glands.

On Monte San Giovanni near San Antiocho at the extreme southwest of the island, a similar but larger form is recorded. I have not found it there but have this larger form from a few kilometres nearer the coast.

Herr Dohrn sent some rather similar specimens to Paulucci giving the locality as 'near Sassari'. These have a wholly white aperture and tend to be more globular and a little conical. She named them *pudiosa*. This form is fairly abundant near Iglesias, 30 km north of San Giovanni but 160 km south of Sassari. Their anatomy also shows a majority in favour of unbranched mucous glands and Pfeiffer treats *pudiosa* as a junior synonym of *isarae*. I am inclined to agree.

From two localities south of Thiesi and only 35 km south of Sassari I have specimens with a slight resemblance to the larger form of *isarae/pudiosa*. I remain doubtful as to the accuracy of 'Sassari' as a locality for *isarae/pudiosa*, except in a rather broad sense.



In the remaining two thirds of Sardinia and two sizeable and three small areas in Corsica where *Marmorana* is found, greater variation in the forms means that racial territories cannot be so clearly defined. The inadequate descriptions and contradictory determinations make it impossible with any certainty to give names to the forms found in such territories.

Leaving over Pfeiffer's one remaining suggested race, and he had doubts about it, I come to Paulucci's forms *suburbana* and *adjaciensis*.

*Marmorana serpentina* form *suburbana* Paulucci 1882.

Although neither are found in the area covered by his hunting, Pfeiffer says much about *suburbana* and *adjaciensis* when dealing with *carae*. He says that both have the yellowish-brown epidermis of *carae* but with some brown in the aperture, *adjaciensis* more widely than *suburbana*. Specimens he saw in the museums from localities in northeastern and northwestern Sardinia were sometimes given one name and sometimes the other, and are so connected with each other by intermediate forms, even from the same locality, and with form *sardica* (Fra Piero) that he feels the three forms can hardly be separated on shell characteristics. I think that is rather too harsh.

However, Hesse in Rossmässler (Neue Folge, vol. 14) quotes Wiegmann's report on the anatomy of two adult and one juvenile *suburbana* found by Maltzan near Macomer, 60 km south of Paulucci's locality of 'near Sassari'. Unlike *serpentina* the pairs of blades on the dart (he also had TWO at most) only curve slightly towards each other and there should be a visible gully between the blades of each pair. I have heard doubts expressed as to this description of the dart and moreover wonder if the evidence of two darts can be treated as conclusive when dealing with anything as given to minor variations as *serpentina*.

The few darts I obtained from 27 specimens from Ghilarza and Abbasanta and thereabouts (15 to 30 km south of Macomer) show no appreciable gulley but on shell characteristics these specimens seem to be *suburbana* as illustrated by Paulucci. For *Marmorana*, the bands on many of my specimens are remarkably prominent and show little interruption by marbling. While the striation is typical, the surface is finely granulate. Within the aperture, the palate is often tinged with pale pink. The area is the volcanic rock between Macomer and Oristano. I found them all under stones.

Germain (1929 and 1930) treats *suburbana* as a separate species on the strength of the variation in the dart, and reports it as occurring at Bonifacio in Corsica on the limestone and the granite. He does not say that the darts of his specimens were examined. I have not seen it at Bonifacio.

Leaving northern Sardinia until later, I turn to Corsica, where limestone is restricted to a narrow strip surrounding Bonifacio in the extreme south and a few other small areas where the presence of *Marmorana* is at least doubtful.

*Marmorana serpentina* form *jaspidea* Moquin-Tandon 1855.

Moquin-Tandon (1855) seems to have based his form on specimens from Bonifacio. His description is 'Shell larger; bands not distinct above, reduced to marblings; colours brighter.' Apart from its size compared with *serpentina*, this could cover any shape of shell. Mabile (1867) gave it a new description and treated it as a separate species. Caziot (1902) accepted this but unjustifiably renamed it *bonifaciensis*. He comments that to separate it from typical *serpentina* 'it suffices to select the larger and more globose shells from the smaller and more depressed ones'. Notwithstanding this he goes on to say that at Bonifacio there are depressed forms of *jaspidea* and a form *minor* . ! ! Caziot gives names to no less than nine forms from the limited area around Bonifacio. Germain (1929 and 1930) reduces this to five, and adds that the value of these forms is purely relative and that intermediates exist. There is plainly no 'race' here but you can, if you wish, select specimens as *jaspidea* as Caziot suggests, or as any of the other forms mentioned by Germain.



Forms of *serpentina* are abundant on the old fortifications at Bonifacio and on the rockwall of the road east towards Gurgazo, on the limestone. They are also reported on the surrounding granite, particularly at La Trinité, to the west. Three hunts there have produced nothing but signs of a fairly recent forest fire.

Caziot (1902) reports *jaspidea* from Cap Corse at the north of the island. He says 'Rogliano. At the junction of the two roads to the village, the new one and that through Giojelli.' There on the narrow spit between the two roads I found the burial place of the Bastani and Bernadi families and on the rockwall opposite there is a form of *serpentina*. 23 mm diameter, 15 mm high; depressly globose with finely detailed marking on an off-white base. It is not granulate. The inner and columellar walls of the aperture are brown. This form is also found under stones near Tommino and in the Meri and Luri valleys a little to the south. The form from this area may be a local race but I would not call it *jaspidea*, at least when compared with the forms from Bonifacio.

Three other Corsican forms need a brief mention.

*Marmorana serpentina* form *cenestinesis* Crosse and Debeaux 1869.

The prime locality for this form is the Foret de Mello high in the mountains above Corte in the centre of the island and under the serpentine rocks nearer the town. The spire seems curiously flattened; the first band is regularly broken into more or less square blocks by narrower white spaces; the gap between the first and second band is pale, if not white. It is reported from Bonifacio and also from the mountainside behind Bastia towards Santa Lucia. I found it at Alzeta nearby, some 300 m higher than the city. I think it is just a colour variety.

I would add that in the Bastia area five more of Caziot's forms are reported, apart from two more which he 'planted' as a colony at the old fort in Toga just north of Bastia. The fort is now gone and the colony seems extinct.

*Marmorana serpentina* form *velanica* Mabilie 1867.

This is a very conical form with six whorls, one more than usual, and six bands. Germain in 1929, his preface being dated 1927, said that he had never seen a specimen. As he mentions it again in 1930, but without that comment, perhaps he saw it in the meantime. I think it is a bit of a freak.

*Marmorana serpentina* form *jaspidea* var. *pseudo-hospitans* Pollonera in Caziot 1902.

After all that I am not going to describe this one. However, in Caziot (1902), because of the existence of a helcid from Peru named *jaspidea* by P. Pfeiffer in 1859 which he thought had priority, Caziot renamed Moquin-Tandon's *jaspidea* as *bonifaciensis*. Germain (1929) points out that P. Pfeiffer's species is an *Epiphragmophora* and that Moquin-Tandon's name has in fact four years priority. Not content with that, Caziot (1902) published a variety *pseudo-hospitans*. Unfortunately, his printer transposed the first two letters and in that form K. L. Pfeiffer (1946) repeated it: '*speudo-hospitans*'. Anyway, these 'Cazioticies' make me feel sick too.

Now back to northern Sardinia.

*Marmorana serpentina* form *adjaciensis* Paulucci 1882.

Paulucci (1882) named this form on specimens sent her from 'near Ajaccio' in Corsica, where no *Marmorana* has since been found. However, the specimen she depicts in her Fig. 3 on plate 6 is said to have come from there. She also records having specimens from Isola Maddalena, just off the extreme north of Sardinia. She treats the form as a variety of *carae* Cantraine. Westerlund (1889) described a high spired form from the Capo Figari just to the southeast, and, in spite of the conflict in dates, refers to its picture published by Kobelt in Rossmässler (1890) (Neue Folge vol. 4. Fig. 518) Form *adjaciensis* is also reported from nearby Isola Tavolara.



I have specimens of a form of *serpentina* from Buoncammino near Santa Teresa and from Arzachena near Palau, both on the mainland near Isola Maddalena and, but more conical, from Telti's old railway station further inland. They all have a strong resemblance to the form found at the mountain at Oliena (called Monte Ortu Camminu on some maps), and to the more brightly coloured one from Monte Albò 40 km to the north and some 70 km south of Capo Figari. The shell is up to 23 mm diameter, 17 mm high; globose and a little conical; at least the upper whorls are finely granulate. The brown mark on the base of the columella spreads rather more than on *suburbana*. The dart is typical of *serpentina*. The yellowish epidermis is however present on my thirty or so specimens. They were found under stones.

K. L. Pfeiffer (1946) found one specimen on the Oliena mountain and one more on Monte Albo, but in the Berlin Museum there were five found by Maltzan at Oliena. He explained away the yellowish-brown epidermis as the result of 60 years in the museum, but at first it lead him to think of them as *suburbana*, which, on my understanding of his remarks quoted earlier, might be taken to include *adjaciensis*. Finally, but not without expressing doubts, he treats the Oliena form as *jaspidea* Moquin-Tandon. I am very doubtful about that identification.

I have not seen specimens from Isola Maddalena, Capo Figari or Isola Tavolara, but if they agree with mine from the other localities, I suggest that they may all be *adjaciensis*. Those from Monte Albo may be 'jazzy' but in the light of the Bonifacio forms, I cannot see them as *jaspidea*.

Form *adjaciensis* is also reported from Corsica at Porto Vecchio near Bonifacio and at Vivario near Corte in the centre of the island.

There remains the northwestern part of Sardinia which might rather loosely be called the area 'near Sassari' from which as already indicated a number of forms have been reported. I think it is best divided into two, the 'Lugodoro' and the 'Northwest Coast'.

#### *The Lugodoro*

The mainly granite area of the Gallura to the west of Santa Teresa and around Tempio Pausania and the adjoining eastern parts of the volcanic area produce very few specimens. In fact I have only found three dead shells. They were at Calangianus at a site devastated by a forest fire shortly before my last visit in April 1979. Further west on the volcanic rocks and on the marls and clays of the Lugodoro proper around Sassari and southwards towards Thiesi, specimens are abundant again. The shells are mostly large, up to 24 mm diameter, 16 mm high, with a well raised spire, rather swollen, occasionally conical, occasionally depressed. The bands are lost in marbling on a white base. There is no granulation or yellowish epidermis. They live exposed to the sun and not under stones. The inner and columellar walls of the aperture are fairly constantly brown. Some of the smaller specimens show some similarity to the smaller specimens from Bonifacio, but the Lugodoro form seems pretty consistent within itself and might constitute a 'race'. However in view of my doubts about the form *adjaciensis* and the confusion in the next area, the 'Northwest Coast', I do not press this or suggest a name.

#### *The Northwest Coast.*

The northwestern coastal area from Bosa and Tresnuraghes through Alghero and Capo Caccia to Monte Nurra and Argentiera, volcanic, granite, alluvium, limestone and more granite produces a variety of smallish forms living openly on walls *etc.* At St. Peter's Church near Bosa the form has some likeness to *isarae* which is reported from 'near Sassari', 75 km to the north. Others are near to *serpentina* itself, or to the Lugodoro form. There is no 'race' here, even to my 'lumper's' eye, but among the forms there should be form *sardica* Fra Piero Arbanasich in Caziot (1902). Fra Piero seems to have been a keen collector of shells which he distributed with his own names and comments attached. He produced a paper on the Limacids of Sardinia but so far as I can discover nothing on *Marmorana*. Caziot (1902) quotes from a letter of Fra Piero's in which the latter says 'True *serpentina* does not occur in Sardinia. There are two forms that come near to it; the variety *sardica* and another to which I give provisionally the name



*subserpentina*.' It is thus particularly unfortunate that Caziot's Sardinian and Corsican collection cannot, as I am told, now be found so that the specimens of *sardica* can be examined.

The Lugodoro form and these northwest coast ones and all the others living exposed to the sun, do not have the yellowish-brown epidermis of *carae*, *suburbana* and *adjaciensis*, which seems to be limited to the forms living most of their time under stones. I wonder if its loss may not be the result of 'defying the sun', and so of doubtful value in distinguishing forms and races. Further, if those fine granulations are merely epidermal, then, without it and ignoring the 'jazzy' colouring and marking, the Monte Oliena and Monte Albo form would be much nearer to the Lugodoro form.

### CONCLUSION

To sum it up, largely following K. L. Pfeiffer (1946) a case can be made out for 'races' within *Marmorana serpentina* with fairly wide but definable areas of distribution in southern Sardinia. A few other similar areas can be added, but there remain the Bonifacio and Northwest Sardinian forms. There are also a small number of specimens that I have found in twos and threes throughout the island that do not really fit into the pattern of areas. To these I would still apply words I used years ago when the Society was still meeting in the Boardroom here and the use, misuse and abuse of varietal names were under discussion; 'When dealing with *Marmorana*, scrap the lot and substitute six-figure map references.'

In these thoughts I have tried to make some sense out of subgenus *Marmorana*, but I give the last thought to Dr. A. Zilch, who, when I had the honour of meeting him recently at the Senckenberg Museum and discussing *Marmorana* said; 'What looks sense in the evening after a day's work, may look nonsense in the morning.'

Finally I must express my thanks to the Authorities at this Museum, at the Muséum National in Paris and at the Senckenberg Museum for putting up with my visitations, but I must add that it might happen again as I go back to Bastia and Bonifacio in Corsica and, not that rude place in the southwest, but Isola Maddàlena in Sardinia on Thursday.

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# THE FUNCTION OF THE SPINES IN *MUREX* (*MUREX*) *PECTEN* LIGHTFOOT AND RELATED SPECIES (PROSOBRANCHIA: MURICIDAE)

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**Abstract:** Spines of *Murex pecten* are strong, solid and sharp-pointed and are developed along the varix of the body whorl and along the anterior canal at each aperture. Three such rows of spines develop on each whorl. Primary spines are large and parallel to the substrate; secondary spines are smaller, nearly perpendicular to the substrate and are best developed along the anterior canal; tertiary spines which are small and inconspicuous, occur at the bases of primary whorl spines. Anteriorly the primary and secondary spines form a cage-like structure. Spines grow by a rapid proliferation of mantle tissue which folds into a C-shaped cross section initially, fills in the spine and is resorbed again. The shell probably grows in relatively short bursts between varices, followed by prolonged periods of no growth at each varix stage. This arrangement of spines is not as well developed in related species, but in all it is precise and involves too complex a growth pattern merely to be decorative.

The spines are generally interpreted as being protective. The precise pattern of three rows of spines per whorl ensures that the shell always adopts a stable orientation with one row mid-dorsal and vertical. The anterior cage provides a protected area for the head and tentacles within which the snails may feed unmolested. In *Murex pecten*, where the cage is best developed, it could be used to contain prey. These functional inferences should be tested by observations of the snails in their natural habitats.

Voss (1961, p. 170) and Tasch (1973, p. 319) have stated that the spines of spinose *Murex* species, like *M. (M.) pecten*, are protective against fish predators, but they give no details. Palmer (1979) has shown that some spines and thickenings of tropical marine shells protect the snails from predation by fish and crustaceans, but the spines he describes and illustrates are very different from those of *Murex pecten*. While it is true that the spines of *Murex pecten* enlarge the shell, making it more difficult and uncomfortable to swallow whole, they have too precise an arrangement for this to be their only effect. Furthermore, most of them are aligned in parallel rows along the anterior canal where they cannot protect the main body of the animal within the shell. Analysis of the precise arrangement of spines has led to the conclusion that, while the spines are primarily defensive, in *Murex pecten* they may have been used to contain food as well. Only direct observations of the species in its natural habitat can confirm this suggestion. Nevertheless, it is reasonable to advance the hypothesis (a) to stimulate the necessary observations and (b) to test the method of analysis (see Carter, 1967, for another such example).

Sound functional interpretations must be based on detailed morphological knowledge. The exact arrangement of spines in *Murex pecten* depends partly on their individual morphology and partly of the growth of the shell. I shall describe the spines first, then shell growth and, finally, discuss the possible functions of the resulting shell shape.

## MORPHOLOGY OF THE SPINES

All spines considered here are sharp-pointed and solid, with a narrow ventral groove. Spines of any one aperture occur in two series (Fig. 1A). Those on the varix I shall call *whorl spines*, those



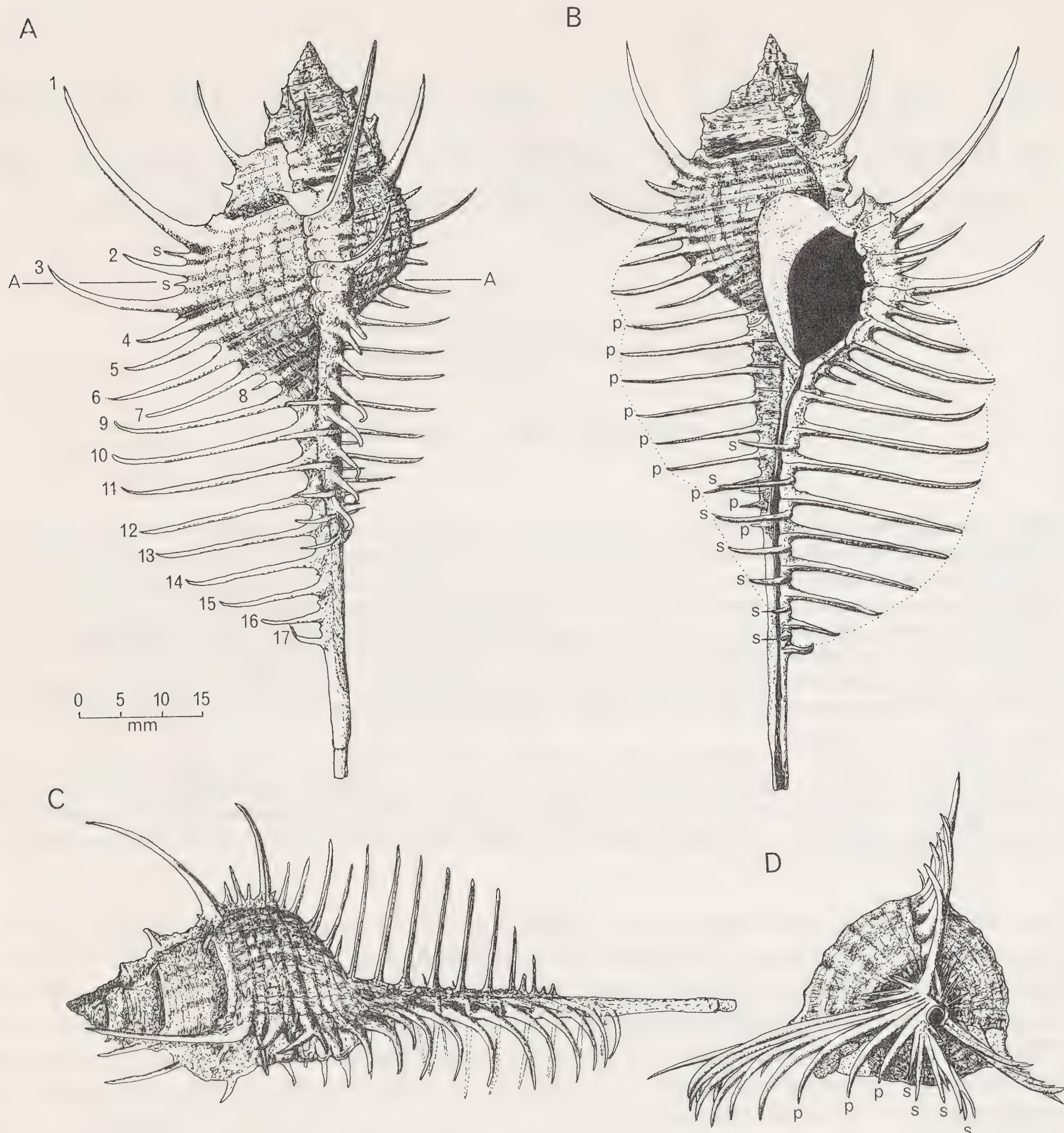


Fig. 1. *Murex (Murex) pecten* Lightfoot. Four views to show morphology and the arrangement of the spines. 1A Dorsal view in life. 1-8 primary whorl spines, 9-17 primary canal spines, A-A axis about which shell balances, s secondary whorl spines. 1B Apertural (ventral) view to show anterior 'cage'. p primary canal spines of antepenultimate aperture, s secondary canal spines of the last aperture. Note that together these spines complete the left hand side of the anterior 'cage'. 1C Lateral view to show that the tips of the primary canal spines turn down and all end at approximately the same level. Outlines of secondary canal spines of the last aperture dotted. 1D Anterior view to show disposition of spines in three series and the arrangement of spines around the front margin of the anterior 'cage'. p primary canal spines of the last aperture, s secondary canal spines of the last aperture. Drawn from photographs of a small complete example from the Andaman Isles, Lancaster coll. Merseyside County Museums.



on the anterior canal, *canal spines*. Within each series primary, secondary and (rarely) tertiary spines can be distinguished on size and orientation. Almost all primary spines are approximately parallel to the plane of the aperture and, by inference, to the substrate (see Linsley, 1977, pp. 196–9). Secondary and tertiary spines are smaller and usually orientated at a high angle to the plane of the aperture (Figs. 1B, 1D). All primary and secondary spines align with ridges on the whorls or anterior canal so that the positions of homologous spines can be traced during the growth of the shell. Although spines are added (and in some species lost) during growth, this accounts for relatively little variation in the number of spines. Where the number of spines varied in the last three apertures, it was always the most anterior primary spine which was added or lost. Starting posteriorly, the spines may be numbered as follows:—

A. *Primary spines* (1–17, Fig. 1A). 1. The largest spine which curves back (i.e. posteriorly) and upwards (i.e. away from the substrate) towards its tip.

2. A smallish spine curved slightly back and ventrally.

3. A second very large backwardly curved spine also turned very slightly down at its tip.

4–8. Five small to medium sized spines which are almost exactly parallel and all have their tips curved strongly down. The last (8) is always short and originates close to the angle between the body whorl and the anterior canal. Usually the middle spine (6) is the longest.

In *Murex pecten* spines 1–8 form the whorl spine series.

9–22 (possibly) A series of 8–14 long, parallel canal spines, all very slightly directed anteriorly and all curving sharply down at their tips (Fig. 1C). Usually 10, 11 or 12 is the longest and the last may curve down steeply (Fig. 1D). All the canal spines terminate at the same level (Fig. 1C) and, as they are parallel and equally spaced, they form one side of an anterior cage which is raised slightly off the substrate.

B. *Secondary spines* (*s*, Figs. 1B, 1D). A few small secondary spines, which are directed obliquely downwards, occur in the whorl spine series. Usually one lies between primary spine 1 and the suture. Further secondary spines may lie between primary whorl spines 1, 2 and 3. In the canal spine series, secondary spines usually alternate regularly with primary spines. The most posterior (between primary spines 9 and 10) may fail to develop in some shells (Fig. 1B). Secondary canal spines are almost parallel to the primary canal spines of the ante-penultimate aperture, or they may be nearly vertical (Fig. 1D). Secondary canal spines all terminate at the same level and, together with the primary canal spines of the ante-penultimate aperture, complete the anterior cage, but on the left side (Fig. 1B). The anterior canal protrudes considerably beyond the front end of this cage.

C. *Tertiary spines* (*t*, Fig. 1B). Very small tertiary spines lie at the bases of primary whorl spines 1, 2 or 3 in some shells. They rarely exceed 2–3 mm in length and are usually directed downwards. They do not align with ridges on the body whorl of the shell.

D. *Spines of related species*. Several related species of *Murex* s.s. have similar sets of spines, but usually not so many nor so elegantly arranged. These species include *M. tribulus* L., the type species of *Murex* s.s., *M. scolopax* Dillwyn, *M. nigrispinosus* Reeve, *M. acanthostephes* Watson and *M. troscheli* Lischke, among others. All are characterized by the presence of both whorl and canal spines, three rows of spines per whorl and very long anterior canals. The principal differences are in the number and spacing of the spines (Plates 9 and 10; Table 2). The spines are usually thicker, often proportionately shorter and always more widely spaced. In *M. tribulus* spine 1 often reaches its maximum development on the penultimate aperture, not the last. In these related species secondary canal spines are reduced so that the anterior cage is not as well developed, but in all the species the primary canal spines are parallel and turn down at their tips.

#### GROWTH OF THE SHELL AND SPINES

Gastropod shells grow by accretion such that increments secreted by the mantle edge are added to the pre-existing shells. Ideally an undamaged shell retains a complete record of its



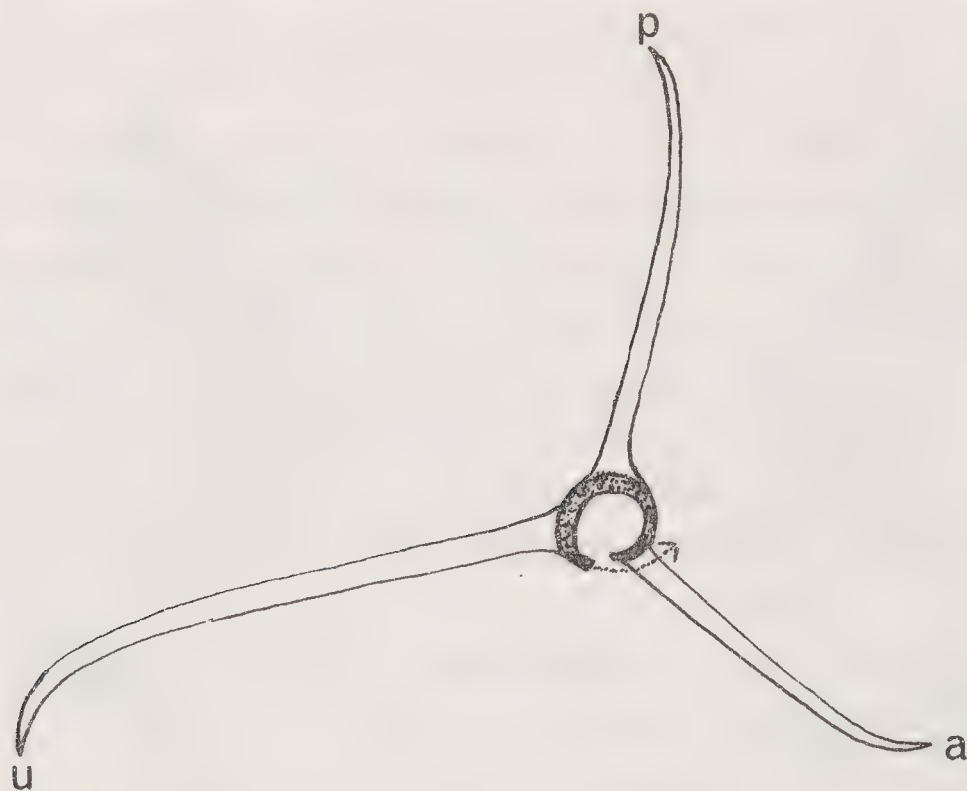


Fig. 2. Diagrammatic section through the anterior canal of *Murex (Murex) pecten* Lightfoot to show the positions of the spines and ventral slit. Further growth of the shell (arrow) must involve resorption of the spines of the antepenultimate aperture. a primary spine of the antepenultimate aperture, p primary spine of the penultimate aperture, u primary spine of the ultimate aperture.

growth, with the shape and positions of former apertures indicated by growth lines. Some snails modify their aperture when mature. They are usually species with a prolonged adult life and the modifications strengthen and protect the aperture. Other snails modify the aperture repeatedly during growth and in these the former positions of the modified apertures form prominent ridges on the shell called varices (singular varix). Muricids typically have varices, which occur regularly at three positions per whorl in the species considered here (Fig. 1D). Since each modified aperture of *Murex pecten* bears spines, these too are arranged in three rows at  $120^\circ$  to each other (Fig. 1D, Plate 9, Fig. 4). Furthermore, because of their different positions on the shell, the whorl spines and canal spines have different histories during growth. Whorl spines 1 and 2 remain, unless damaged, throughout the entire life of the snail. In *Murex pecten* spine 1 often projects just beyond the tip of the spire so that any approach from the rear of the snail is guarded by a whole set of these spines. All spines anterior to spine 2 are resorbed eventually and remain for only three successive growth increments (Fig. 2). Carriker (1972) gives an account of spine resorption in other species of *Murex*.

Shells of *Murex pecten* are common objects in collections and shell shops, but I have yet to see one which died or was collected between modified aperture. While it is possible that collectors and dealers reject such individuals, it seems more likely that they are very rarely found in this state. A sample of about 500 *Murex trapa* recently acquired by the British Museum, Natural History, contained only about 2% of individuals between varices. The most obvious explanation is that the shells grow in short bursts, adding  $\frac{1}{3}$  whorl, modifying the new aperture and then remaining at that growth stage for a long period. Mackenzie's (1961) observations on

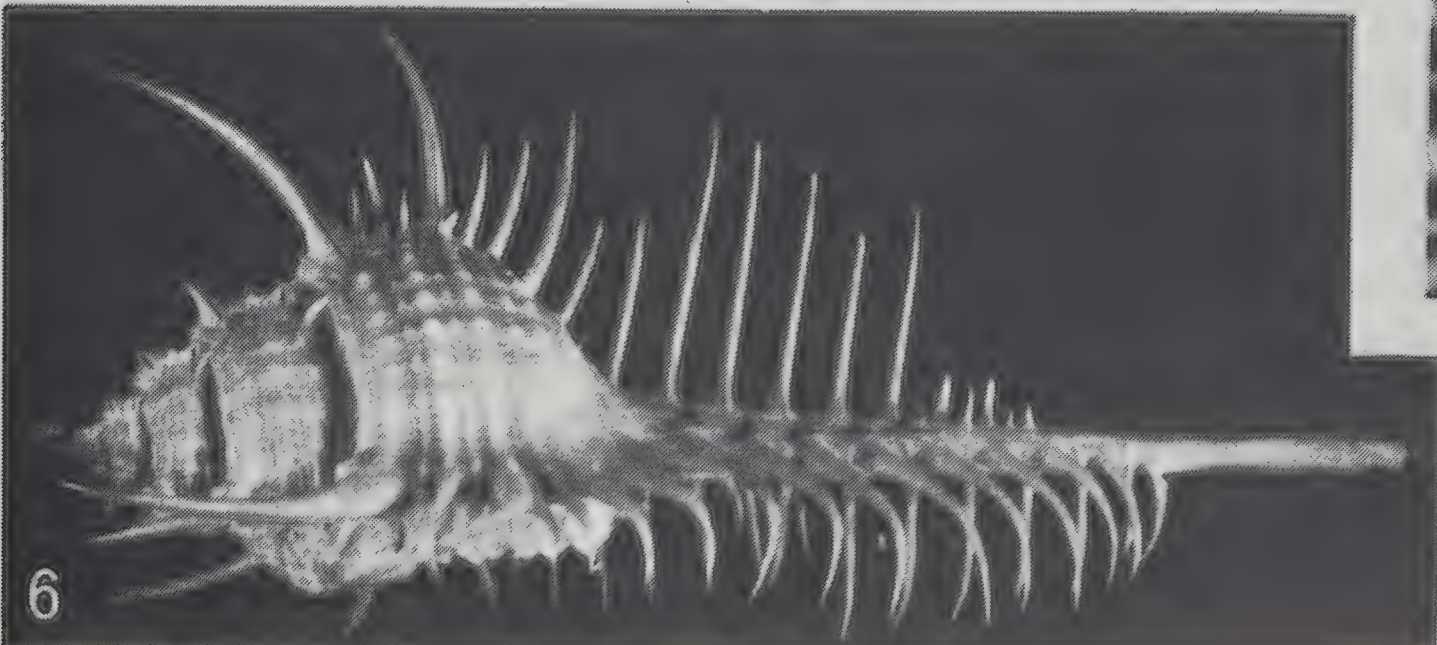
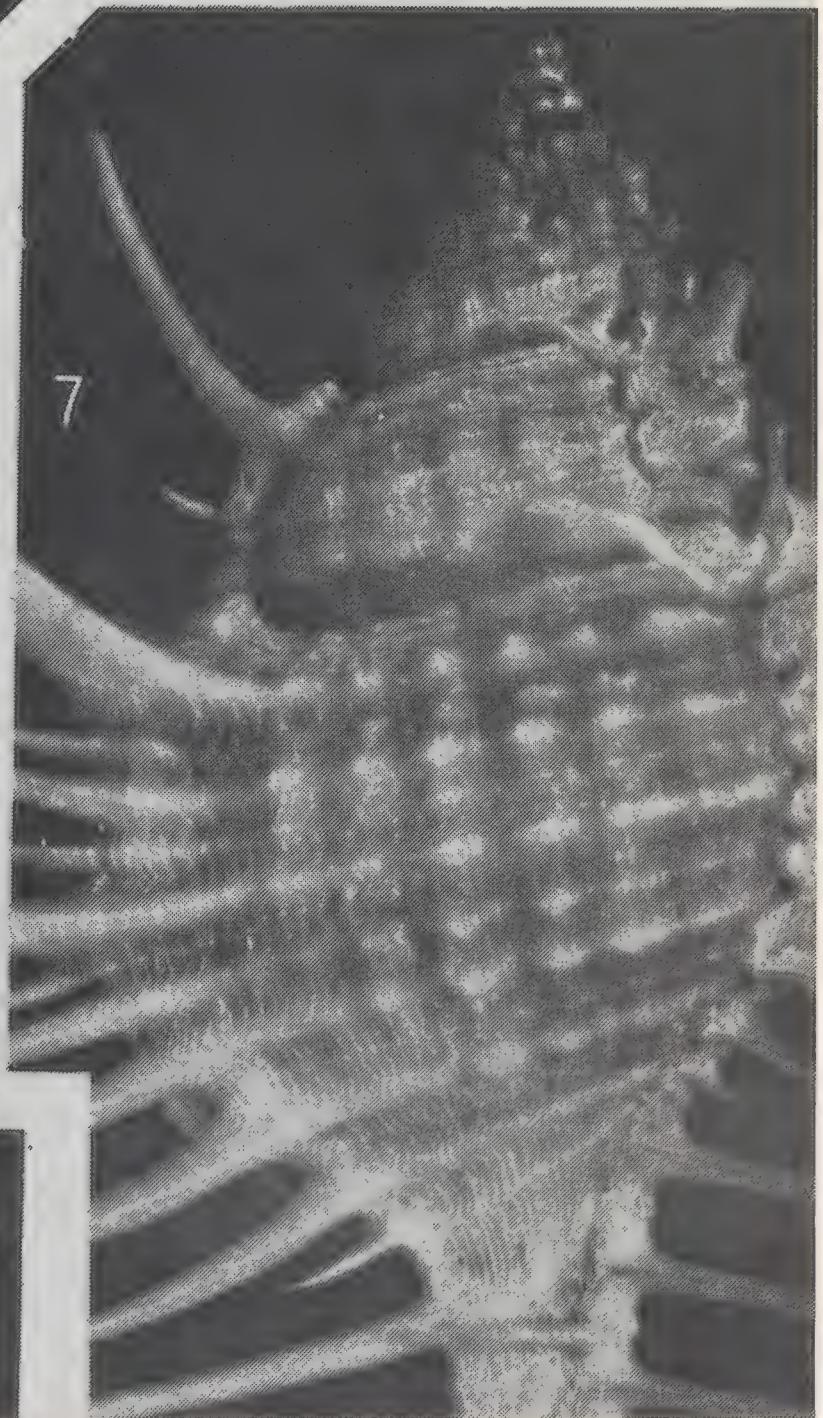
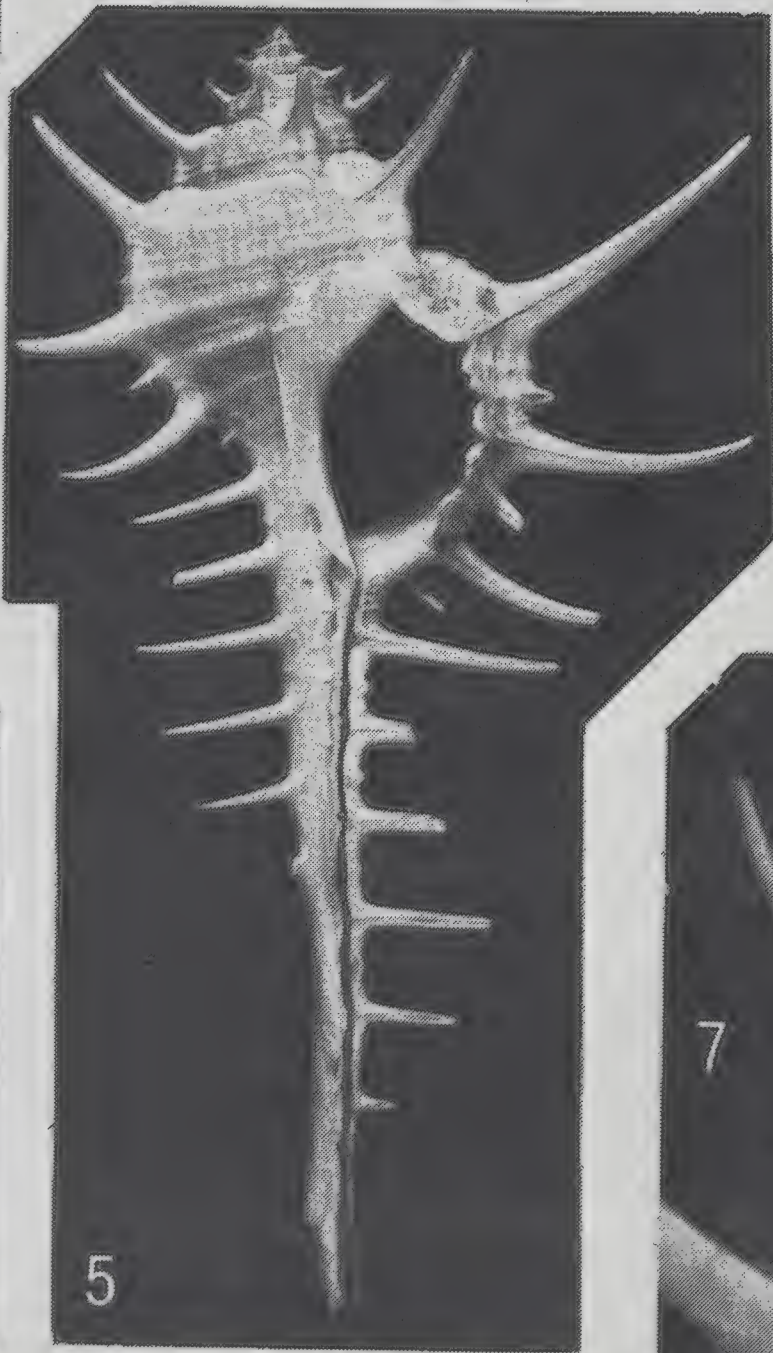
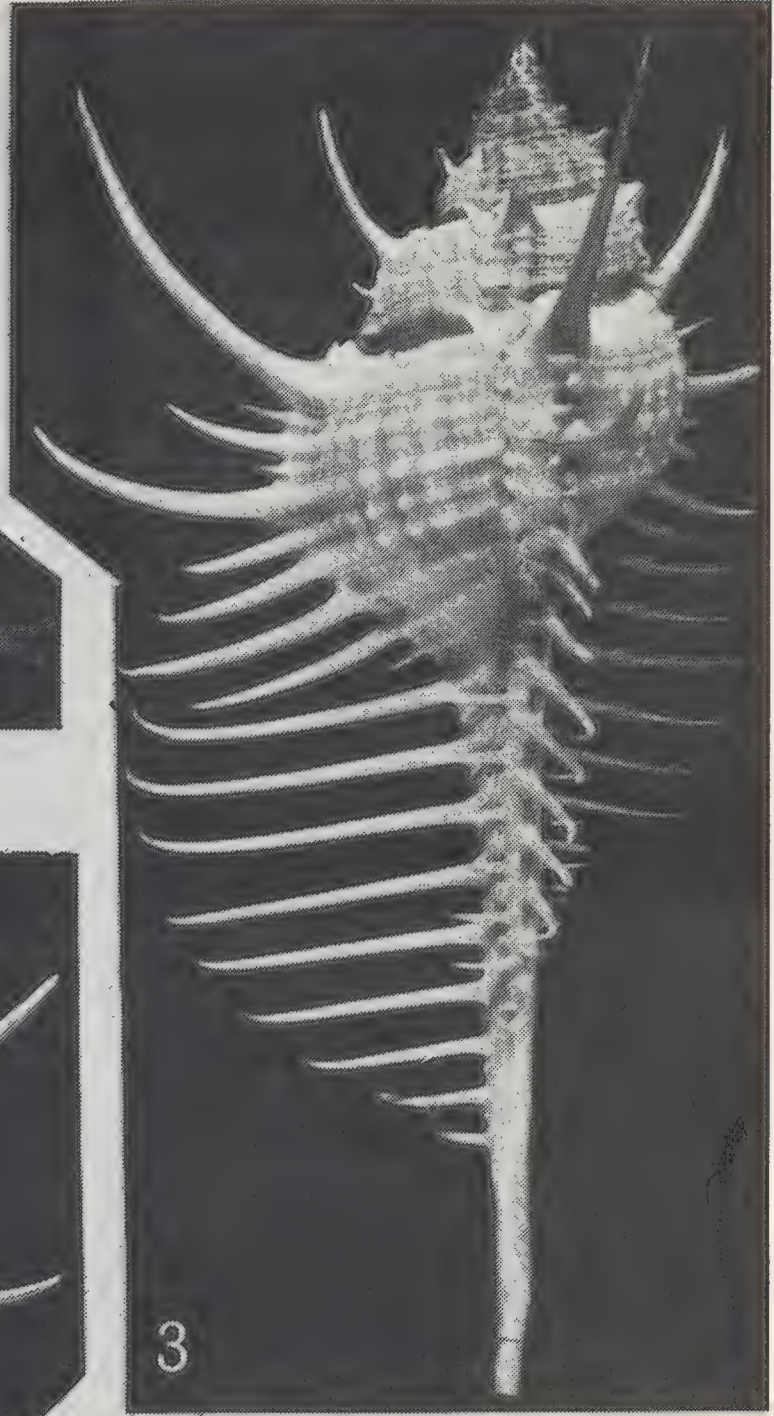
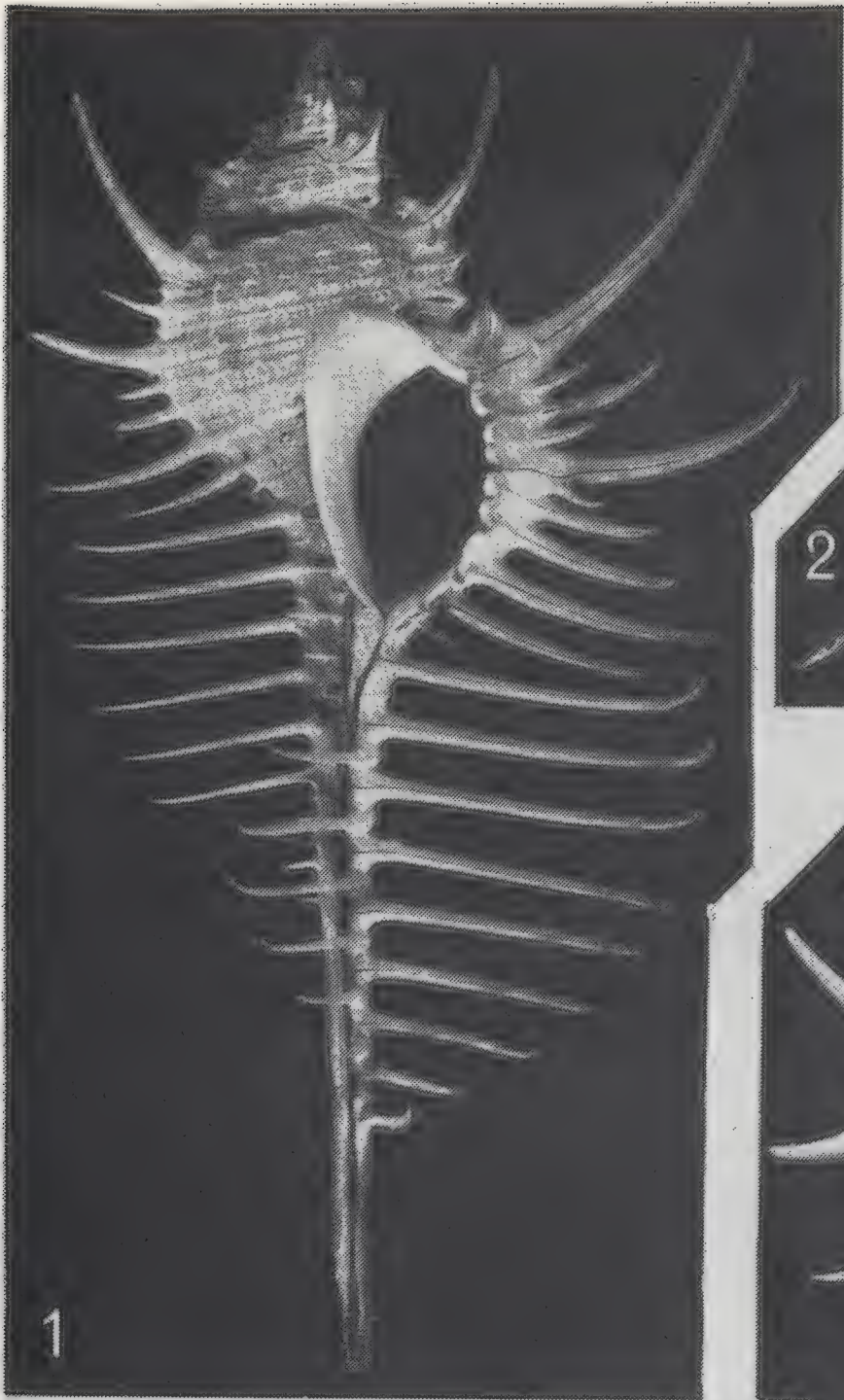
#### PLATE 9 MUREX (MUREX) PECTEN AND M. (M.) TRIBULUS

Plate 9 (opposite) Figs. 1–4, 6–7 *Murex (Murex) pecten* Lightfoot, Andaman Isles. Fig. 1. Apertural view to show anterior 'cage' and whorl spines. Fig. 2. Posterior view to show arrangement of three varices per whorl. Fig. 3. Dorsal view to show mid-dorsal row of spines. Fig. 4. Anterior view to show arrangement of primary and secondary canal spines to form anterior 'cage'. Fig. 6. Lateral view to show primary canal spines all ending at approximately the same level. Fig. 7. Details of last growth increment to show fine growth lines and the ridges which correspond to the primary and secondary whorl spines.

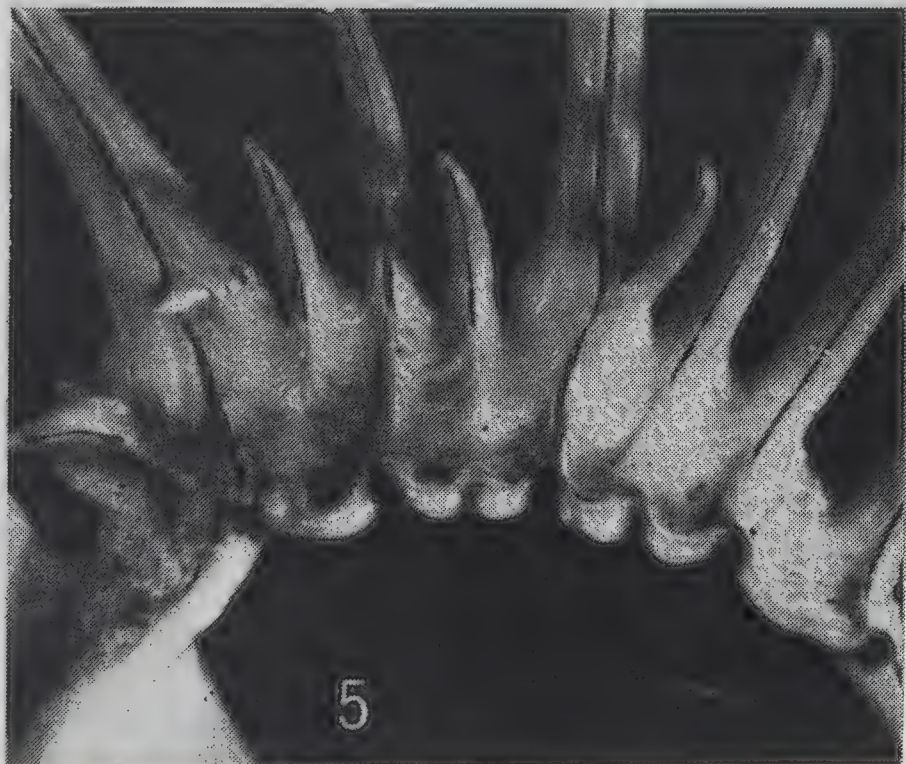
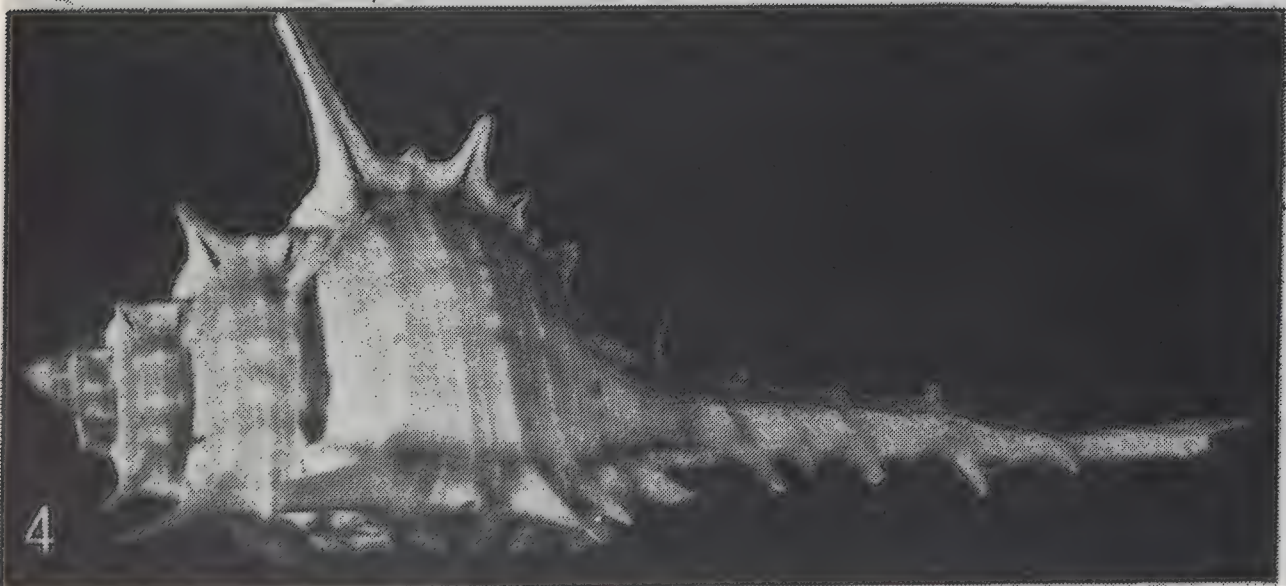
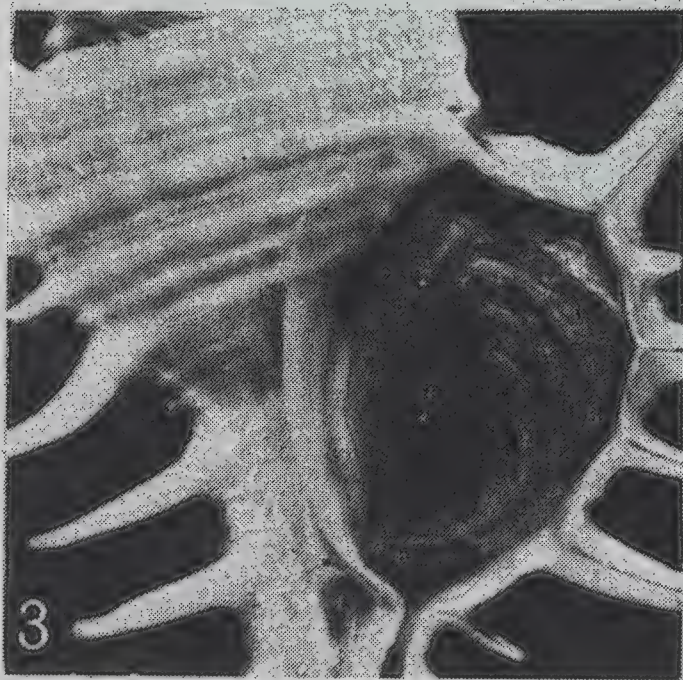
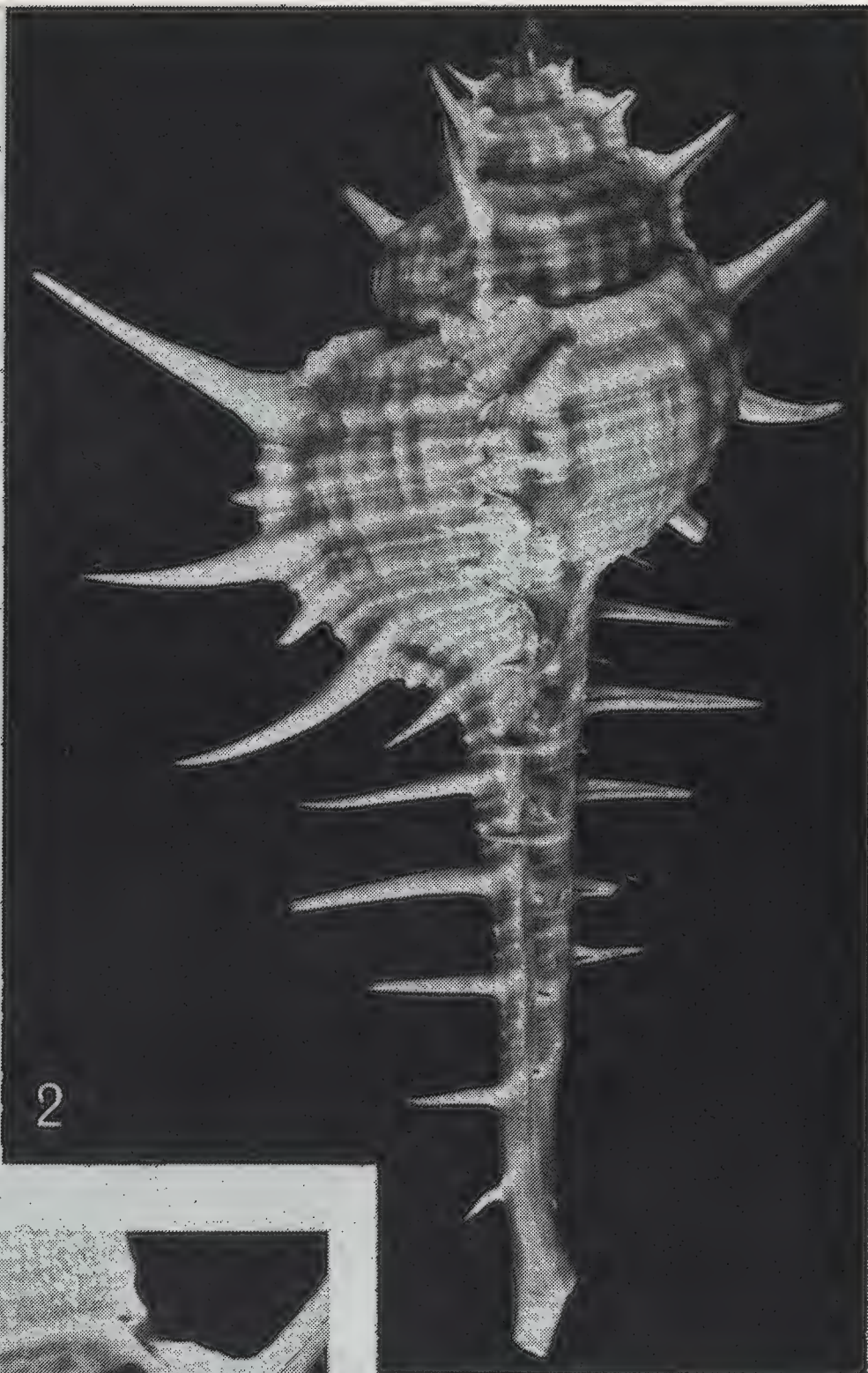
Fig. 5. *Murex (Murex) tribulus* Linn. Apertural view to show similar arrangement of spines, fewer of which are developed than in *M. (M.) pecten*.

Figs. 1–6,  $\times 1$ , Fig. 7,  $\times 2$ . Both specimens in Merseyside County Museums.











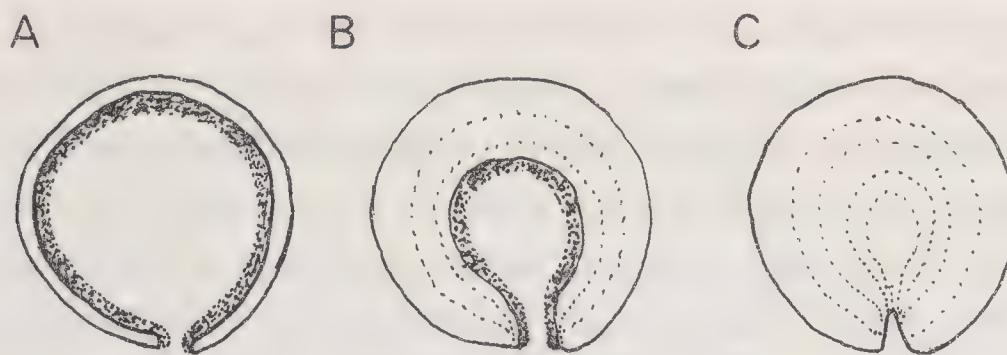


Fig. 3. Diagrammatic sections through a spine of *Murex pecten* Lightfoot, to show inferred mode of growth. 4A Initial stage with periostracum lined by mantle tissue (stippled). 4B Later stage with thicker shell layer. 4C Completed growth showing ventral groove left after the mantle tissue has withdrawn.

the growth of the muricid, *Eupleura caudata* (Say), confirm this. *E. caudata* grows forward half a whorl at a time, secreting a thin shell in about three weeks and then thickening it internally for a further month. It appears that young, rapidly developing *Eupleura* grow only once or twice a year in summer months. Certainly their shells enlarge in about three weeks and then remain at that size for at least 3–4 months, sometimes longer. Opercula of *Murex pecten* show prominent growth lines raised like flanges on the external surfaces (Plate 10, Fig. 3). This tends to confirm that the shells enlarge rapidly and then remain static for long periods. Laxton (1970) describes similar growth patterns in cymatiid snails which, although not closely related to muricids, are characterized by repeated varices.

If growth were accompanied by cryptic behaviour it would account for the scarcity of 'partly grown' shells. Carriker's (1972, pp. 70–71) description of growth in *M. brevivfrons* Lamarck confirms this idea. In *M. brevivfrons* the growth period lasted for 35 days, but most of the shell growth between varices was achieved between 18 and 31 days after feeding ceased and the snails hid (i.e. in two weeks). Carriker gives no indication of how long *M. brevivfrons* remains between growth periods, nor does he state whether the shell was thickened internally after the new varix was formed.

Shells of *Murex pecten* have fine, closely spaced growth lines between varices (Plate 9, fig. 7). Growth was achieved by the addition of small increments, 40–60 of which lie on the last  $\frac{1}{3}$  whorl between the penultimate lip and the dorsal side of the last varix. Although the time interval between these growth lines is unknown, if it were tidal or daily, it would imply a similar growth period to those of *E. caudata* and *M. brevivfrons*. On approaching a new varix, the mantle epithelium of *Murex pecten* must proliferate into long extensions, one for each spine. These curl in on themselves to produce a C-shaped cross section with the opening of the C ventral. The mantle then calcifies the spine from the inside until only a narrow ventral slit remains (Fig. 3). The mantle epithelium lining the ventral slit is then resorbed, starting at the tip, and eventually the connection of the spines to the body whorl or the anterior canal is sealed off. This produces a discontinuity in the growth lines of the shells (Plate 10, Fig. 5). Finally, the shell grows forward about 1 mm to form the outer lip of the functional aperture. This considerable proliferation and resorption of mantle tissue and the fact that most spines are resorbed one whorl after they are secreted, wastes energy. There is, to my mind, no way in which selection could maintain such a complex pattern of growth if it did not confer some advantage on the snails.

#### PLATE 10 *MUREX (MUREX) PECTEN*, *M. (M.) SCOLOPAX* AND *M. (M.) SP.*

Plate 10 (opposite) Figs. 1, 5 *Murex (Murex) pecten* Lightfoot. Fig. 1. A large example from the Andaman Isles with deformed whorl spines on the last aperture. Fig. 5. Detail of the outer lip of the small example figured on Plate 9, to show ventral groove of spines and the growth lines of the outer lip.

Figs. 2–3 *Murex (Murex) scolopax* Dillwyn. Fig. 2 Dorsal view of a small example from the Phillipines to show spines. Fig. 3. Detail of the aperture of a young example from the Red Sea showing prominent growth lines on operculum.

Fig. 4. *Murex (Murex) sp.* Puri, Cultock, E. India. Lateral view to show single prominent mid-dorsal spine.

Figs. 1, 2, 4  $\times 1$ , Fig. 3  $\times 1.5$ , Fig. 5  $\times 2$ . All specimens in Merseyside County Museums.



To summarize, the spines of the current aperture of *Murex pecten* are arranged in a primary series along the varix and anterior canal, which are nearly parallel to the substrate, and a smaller secondary series which are often nearly perpendicular to the substrate. Since modified apertures form three times per whorl during growth, three rows of primary spines result. Two rows form a broad stable base for the shell and anteriorly a cage, while the third is always orientated as a mid-dorsal ridge. The precise function of any one spine is therefore dependent upon the particular stage of growth.

#### FUNCTION OF THE SPINES

A. *General considerations.* Vermeij (1979, p. 686) has outlined morphological features of shells that protect snails from predation by fish and crustaceans which crush or open the shells. Palmer (1979, Fig. 7) has illustrated typical shapes for spines which protect snails against fish predation by enlarging and strengthening the shell. These spines are short, blunt, very thick or broad-based, and radially arranged. The spines of *Murex pecten* are long, thin, solid and most are parallel to each other. Although they enlarge the shells very considerably making it more difficult for a fish to get the shell into its mouth, their form and arrangement do not correspond to the requirements of protection against mollusc-crushing fish. More spines lie along the anterior canal than on the body whorl where most of the soft tissue is housed and those that do lie on the body whorl would be better radially arranged whereas spines 4–8 are parallel (cf. Figs. 4A and B). Whorl spines would be more effective if disposed all over the shell, as sea urchin spines are for example, rather than in three rows. Spines and frills of species in the related genera *Hexaplex* and *Muricanthus* more closely approach this distribution so that it is not rendered impossible by the mode of growth of muricids. Finally, although the three rows of spines ensure that one row always points upwards, a single short spine would suffice (as for example in Plate 10, Fig. 4). Protection against predation by enlarging the shell will not account for the arrangement of spines in *Murex pecten*.

B. *Function of the spines in Murex pecten.* The arrangement of the primary and secondary spines to form the anterior cage is very characteristic and is probably the key to the function of the spines. The arrangement has two effects. First, it provides a broad stable base for the shell, which can

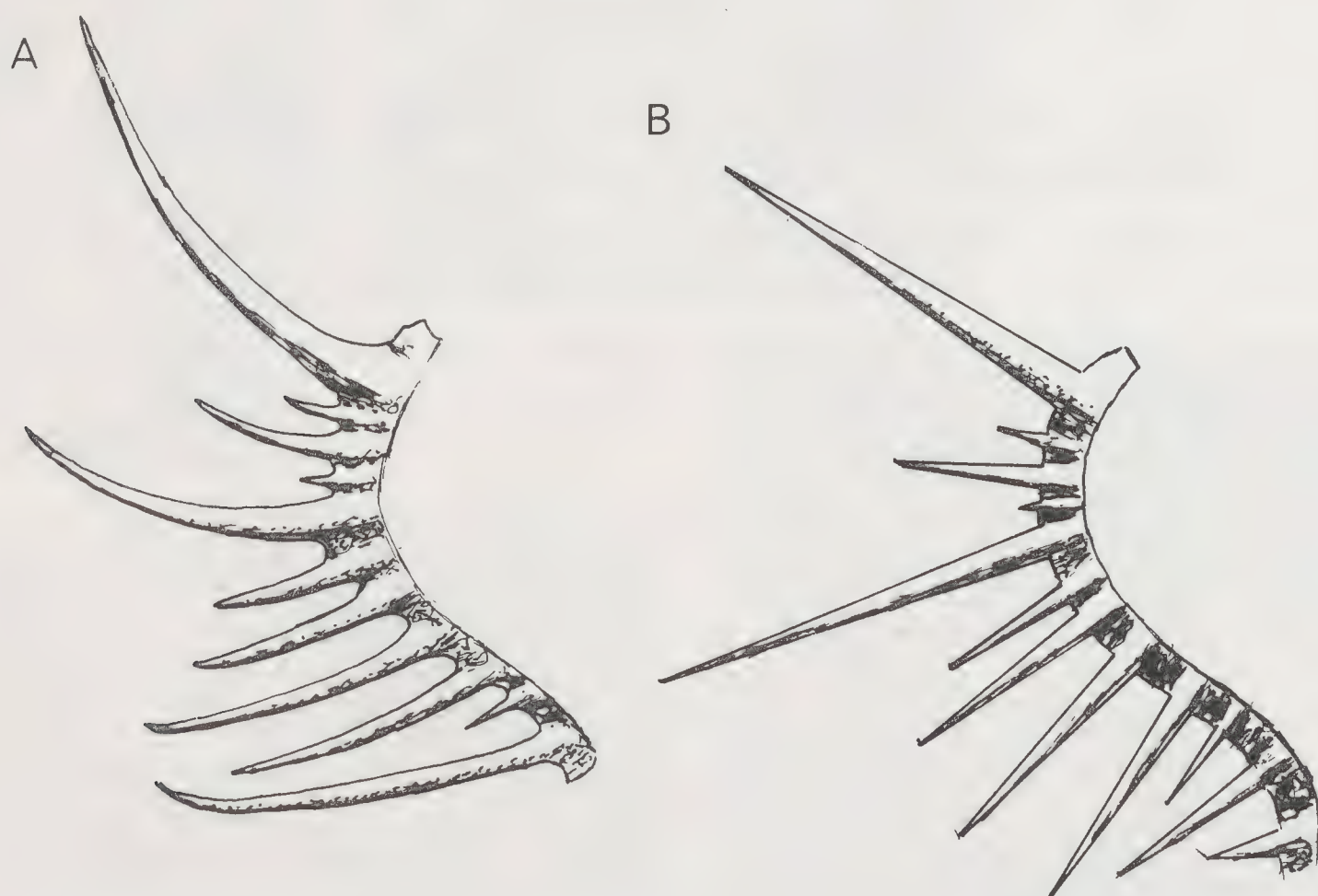


Fig. 4A Arrangement of whorl spines in *Murex pecten* Lightfoot. 4B Idealized protective arrangement of spines in which all protrude perpendicular to the surface.



only be overturned with difficulty, and a mid-dorsal row of sharp protective spines. Even if overturned, the shell will always come to rest with a nearly vertical mid-dorsal row of spines. Palmer (1977) has shown that another muricid with three varices per whorl, *Ceratostoma foliatum* (Gmelin), does not naturally assume a stable orientation as it falls through water. This significantly increases the chances of it eventually landing aperture down. The frill-like varices of *C. foliatum* are interpreted as protecting the snails if they are dislodged from the substrate and fall through the water. However, the spines of *Murex pecten* do not resemble the frills of *C. foliatum* and it is unlikely that they could act in this way.

Secondly, if the shell is clamped against the substrate (the most widespread snail response to danger) it produces a caged enclosure anteriorly. Not only do the head and tentacles lie inside the cage, but feeding must also take place within it. This effect can be tested by comparing the actual shell morphology with that of the ideal design, or paradigm (see Rudwick, 1964) for a cage.

Any area can be effectively enclosed, without using a solid partition, either by a mesh or a grille (Fig. 5). Chicken wire and the bars of zoo cages are familiar examples. To be effective the size of the gaps must be small enough to prevent passage of what is to be caged or excluded. Ideally the gaps should all be the same size since producing smaller gaps wastes constructional material. The spines of the anterior cage of *Murex pecten* form a grille and meet the requirements of the appropriate paradigm almost exactly. Whorl spines 4–8 are parallel, evenly spaced and no large gaps develop between them. The potentially larger gap posterior to spine 4 is sealed by a secondary spine and any approach from a still more posterior angle is guarded by spines 1 and 3 which curve backwards. Spine 8 is short and occurs at the angle between the varix and the anterior canal. Were it to grow as long as adjacent spines, it would produce a much narrower space or even impinge on spine 9 (Fig. 1A). Furthermore, the tip of spine 8 is usually positioned exactly at the point where the gap between spines 7 and 9 equals that between the canal spines. The latter spines are also parallel and nearly equally spaced (Table 1). The table shows that the spacing of primary canal spines tends to be reduced anteriorly. If there were any systematic variation in spacing, one would expect the closest spacing, and hence the maximum protection, posteriorly where the snail's head is. However, the closer spacing is necessary to complete the protection around the front margin of the cage (Fig. 1D). If the horizontal spacing of the spines were maintained exactly, then the short vertical tips of the most anterior spines would be more widely spaced (see Figs. 1A–B). The secondary canal spines of the last aperture continue the cage on the left side. Since they alternate with the primary canal spines, their spacing is also equal. Towards the posterior left of the cage the primary spines of the ante-penultimate aperture complete the cage back to the body whorl (Fig. 1A–B). Indeed in examples where the first secondary spine of the last aperture is missing (e.g. Fig. 1B) this corresponds exactly to the

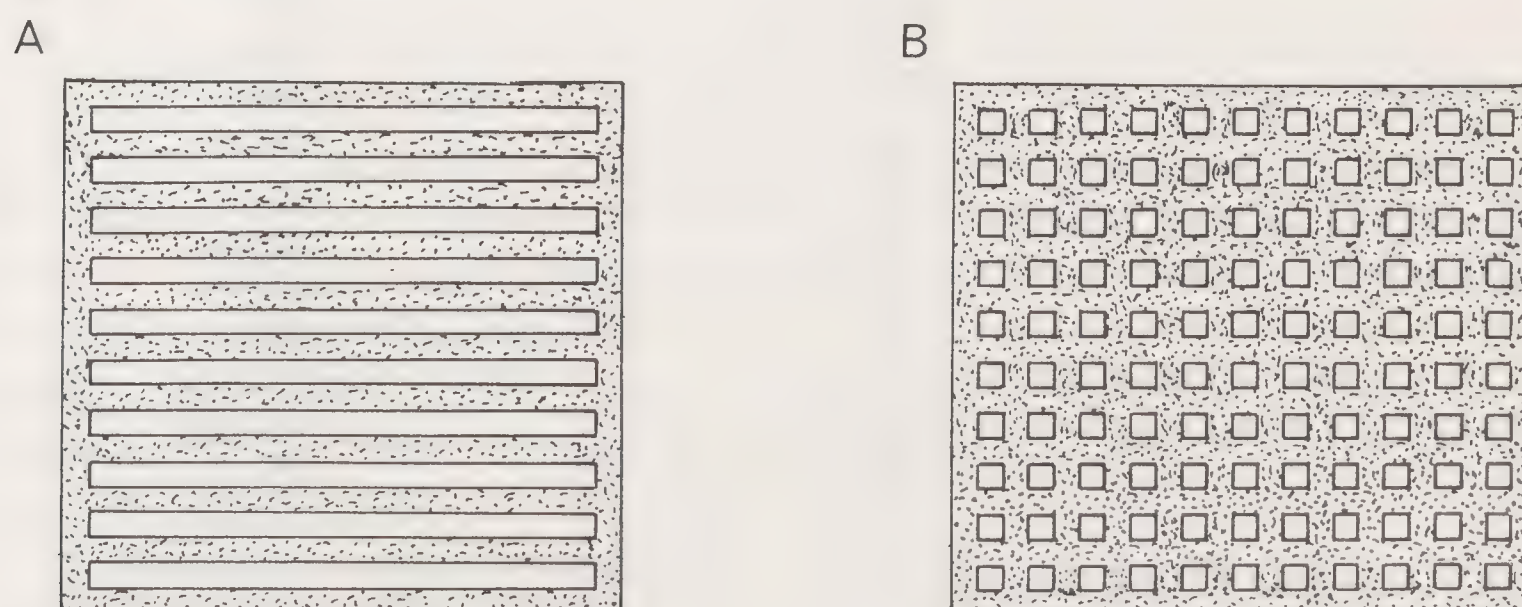


Fig. 5. Ideal grille (A) and mesh (B).



TABLE 1  
Spacing in mm of primary canal spines in *Murex (Murex) pecten*

| Specimen          | shell<br>length<br>(mm) | spines |     |     |     |     |     |     |     |     |     |     |    |
|-------------------|-------------------------|--------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|----|
|                   |                         | 9      | 10  | 11  | 12  | 13  | 14  | 15  | 16  | 17  | 18  | 19  | 20 |
| T. Pain coll.     | 87.0                    | 2.6    | 2.8 | 2.9 | 2.8 | 2.7 | 2.5 | 2.4 | 2.4 | 2.3 | 2.3 | —   |    |
| MCM Andaman Is.   | 91.5                    | 2.5    | 2.6 | 3.0 | 2.5 | 3.0 | 2.7 | 2.6 | 2.0 | —   | —   | —   |    |
| BMNH N. Australia | 106.5                   | 2.7    | 2.6 | 2.7 | 2.6 | 2.4 | 2.6 | 2.5 | 2.3 | 1.9 | 2.0 | 2.5 |    |
| MCM No data       | 111.5                   | 3.9    | 4.5 | 4.1 | 4.6 | 4.4 | 3.7 | 3.3 | —   | —   | —   | —   |    |
| MCM Andaman Is.   | 119.5                   | 4.2    | 4.1 | 4.0 | 4.0 | 4.1 | 4.1 | 3.7 | 3.7 | —   | —   | —   |    |
| MCM Andaman Is.   | 131.0                   | 3.5    | 3.9 | 4.0 | 3.8 | 4.0 | 3.8 | 3.3 | 2.8 | —   | —   | —   |    |
| MCM Moluccas      | 137.0                   | 2.3    | 2.9 | 3.2 | 3.3 | 2.8 | 2.7 | 2.8 | 2.5 | 2.3 | 2.1 | 2.1 |    |
| T. Pain coll.     | 138.0                   | 3.5    | 4.2 | 4.3 | 4.1 | 3.0 | 4.0 | 4.0 | 3.4 | —   | —   | —   |    |
| T. Pain coll.     | 142.0                   | 3.8    | 4.0 | 4.4 | 4.0 | 4.0 | 4.0 | 3.5 | 3.0 | 2.9 | 2.0 | —   |    |
| BMNH Trincomali   | 143.0                   | 4.0    | 4.0 | 4.0 | 4.1 | 3.6 | 3.5 | 3.5 | 3.3 | 2.6 | —   | —   |    |
| BMNH No loc.      | 143.0                   | 3.7    | 4.2 | 4.5 | 4.8 | 3.8 | 3.4 | 4.0 | 3.2 | 3.0 | —   | —   |    |
| MCM Andaman Is.   | 143.5                   | 3.7    | 4.0 | 4.0 | 4.0 | 4.0 | 3.7 | 3.5 | 3.3 | 2.8 | —   | —   |    |

TABLE 2  
Critical diameter in *Murex* species

| Species                  | Shell<br>(mm) | Critical diameter<br>range | (mm)<br>mean |
|--------------------------|---------------|----------------------------|--------------|
| <i>M. pecten</i>         | 87.0          | 2.3–2.9                    | 2.57         |
|                          | 91.5          | 2.0–3.0                    | 2.60         |
|                          | 106.5         | 1.9–2.7                    | 2.43         |
|                          | 111.5         | 3.3–4.6                    | 4.06         |
|                          | 119.5         | 3.7–4.2                    | 3.88         |
|                          | 131.0         | 2.8–4.0                    | 3.56         |
|                          | 137.0         | 2.1–3.3                    | 2.64         |
|                          | 138.0         | 3.0–4.3                    | 3.81         |
|                          | 142.0         | 2.0–4.4                    | 3.56         |
|                          | 143.0         | 2.6–4.0                    | 3.62         |
|                          | 143.0         | 3.0–4.8                    | 3.85         |
|                          | 143.5         | 2.8–4.0                    | 3.67         |
|                          | 41.5          | 2.0–3.8                    | 2.65         |
|                          | 61.5          | 3.2–4.2                    | 3.63         |
| <i>M. scolopax</i>       | 102.5         | 5.6–6.6                    | 6.25         |
|                          | 104.5         | 5.5–6.3                    | 6.00         |
|                          | 108.0         | 4.6–6.5                    | 5.44         |
|                          | 134.0         | 8.5–9.5                    | 8.80         |
|                          | 143.0         | 4.5–5.7                    | 5.60         |
|                          | 88.0          | 4.6–6.0                    | 5.14         |
| <i>M. nigrospinosus</i>  | 89.5          | 6.0–7.3                    | 6.43         |
|                          | 109.0         | 4.0–6.6                    | 5.17         |
|                          | 87.0          | 3.0–5.9                    | 4.40         |
| <i>M. tribulus</i>       | 108.0         | 7.0–10.0                   | 8.33         |
|                          | 110.0         | 5.2–11.8                   | 8.10         |
|                          | 131.0         | 7.4–8.3                    | 7.80         |
| <i>M. troscheli</i>      | 142.0         | 5.5–8.5                    | 7.03         |
|                          | 157.0         | 6.4–8.5                    | 7.17         |
| <i>M. acanthostephes</i> | 79.0          | 3.0–4.6                    | 4.00         |
|                          | 92.0          | 4.0–6.3                    | 5.10         |



point where the primary canal spines of the ante-penultimate aperture start to form the left margin of the cage. Occasionally spines are bent and do not conform to this equally spaced ideal (e.g. Plate 10, Fig. 1), but this is usually an individual abnormality which develops on a single aperture and is not repeated. Such examples represent accidental damage at the critical stage when the spines were first being formed and quite possibly result from predation.

Only in *Murex pecten* does the cage correspond almost exactly to the paradigm. In this species the critical spacing of the canal spines is half or less of that in related species (Table 2) and is so small (4 mm at most) that it cannot be effective against whole fish, only their snouts. No fish small enough to penetrate the cage would pose a threat to a *Murex*. Therefore, I suggest that in general the cage protects the snails within from being attacked, or robbed of their food by opportunistic fish. However, it seems unlikely that *Murex pecten* suffers from a form of predation or competition for its food that the other species do not. This will not explain why *Murex pecten* alone has a complete cage with a low critical spacing. More likely, *M. pecten* uses its cage in some unique way. If the cage were normally raised well off the substrate during locomotion, as apparently occurs in *M. acanthostephes* (see below), it could be used to trap or contain prey when clamped against the substrate. Any food larger than the gap between the spines would be unable to escape and could also be eaten without being removed by fish. The critical spacing of 4 mm or less is more likely to reflect prey size than predator size. If fish merely peck at the snails one would expect them to withdraw and clamp the aperture against the substrate. A cage of spines is unnecessary unless they are exposed out of their shells for prolonged periods. Quite possibly this happens while they are feeding, but their precise food is unknown. Almost 75% of specimens of *M. trapa* and *M. aduncospinosus* opened by Dr. John Taylor had empty stomachs or only sediment in the rectum. Where stomach contents were recovered, they seem to consist of molluscan tissue, although detailed analysis has yet to be completed. Feeding experiments on captive specimens were similarly inconclusive. The shells of both species are not as spinose as those of *M. pecten*.

C. *Shell elevation and balance.* The only illustrations of living *Murex* with spines that I have come across are those of Solem (1974, Plate 5, top figure); Coleman (1975, Fig. 588, p. 209) and Linsley (1978a, Fig. 10, p. 437). The first two illustrate *M. acanthostephes*, the last *M. scolopax*. These figures show that the shell is held well above the substrate by a strong muscular pedal stalk. Such a posture avoids snagging the long anterior canal on irregularities of the substrate. Inevitably the anterior canal is held more or less parallel to the substrate as any other orientation would require considerable energy to maintain it. Not surprisingly, shells of *Murex pecten* balance about an axis which passes from side to side through the middle of the aperture (A-A, Fig. 1A). [See also Linsley, 1977, pp. 199–200 on the balancing of shells about an antero-posterior axis.] The figures also show that when active, most of the tentacles and all of the head lie beneath the cage of spines.

D. *Function of the spines in related species.* Only in *Murex pecten* is there a parallel set of whorl spines (4–8). Other species are characterized by three large radiating spines with two or three smaller spines in between. Only in *M. pecten* is the cage fully developed with no larger gaps around its periphery. I suggest that if the cage is ever used to contain prey, only *M. pecten* does this. In the other species the spines still have their protective effects. Indeed the three large whorl spines (1, 3 and 6) more closely approach the expected arrangement for protection against mollusc-crushing fish (Fig. 4B).

Anteriorly related species have fewer primary spines which are stouter and more widely spaced. Again this makes them stronger for mechanical protection, but less useful in forming a cage. Secondary canal spines are reduced in some examples of *Murex troscheli* and *M. tribulus*, and thus their cages are incomplete anteriorly. The most anterior canal spines are often the most widely spaced and in some examples of *M. troscheli* and *M. scolopax* the number of primary canal spines is reduced during the later stages of growth. All these points indicate that the spines of these related species are at most defensive and simply act to protect the snails beneath.



## ACKNOWLEDGEMENTS

I am grateful to Dr. P. Mordan, British Museum, Natural History; Dr. I. Wallace, Merseyside County Museums and Mr. T. Pain, for the loan of, or access to, specimens. Dr. J. Taylor, Mr F. Woodward and Miss Linda Jobson contributed valuable discussion. The former also drew my attention to relevant publications and provided unpublished data on growth and food of *Murex trapa* and *M. aduncospinosus*. Mrs K. Smythe kindly provided information on habitats for species which occur in the Arabian Gulf, while Mr. D. Birch, Liverpool University, helped with the photography.

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# THE MODE OF LIFE AND FUNCTION OF THE SHELL BUTTRESS IN *CUCULLAEA CONCAMERATA* (MARTINI) (BIVALVIA: ARCACEA)

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(Read before the Society, 15 November, 1980)

*Abstract:* *Cucullaea concamerata* (Martini 1777) (syn. *C. granulosa* Jonas 1846) possesses a posterior buttress in each valve. The function of this structure has been investigated and it is concluded that it reduces the length of (thereby assisting valve alignment), and the effect of shear upon, in particular, the 'catch' component of the posterior adductor muscle. The shell of *Cucullaea* is inflated and the posterior face is antero-posteriorly flattened, so that this region lies flush with the surface of the sand. These are adaptations to this species' mode of life, conferring stability in an unstable niche. The buttress was a necessary co-requisite of these modifications. Buttresses of *Cucullaea* and members of the Laternulidae are compared and shown to be of quite different function; the buttress of *Cucullaea* is more meaningfully compared with the septum of members of the Dreissenacea which fulfils very similar functions.

## INTRODUCTION

The external ribbing of a bivalve may also be seen internally. Sulcations or folds are also represented internally and often serve as platforms for muscle attachment. In two major extant bivalve groups, however, namely representatives of the Anomalodesmata and the Arcacea (both ancient lineages) a strengthening rib or buttress occurs on the posterior face of each valve.

In the Anomalodesmata, a buttress is seen in members of the Periplomatidae and Laternulidae. These two families are closely related (Boss, 1978), the former representative of more primitive conditions, and are usually placed in the Pandoracea Rafinesque 1815. Recently, however, Morton (1981c), has removed these two families from the Pandoracea and relocated them in a new superfamily—the Thraciacea Stoliczka 1870. The structure and function of the buttress in the Laternulidae Hedley 1918 and Periplomatidae Dall 1895 has been reviewed by Morton (1976; 1981a).

A buttress with a superficially similar structure occurs in *Cucullaea concamerata* (Martini), a representative of the rare family Cucullaeidae Stewart 1930 in the superfamily Arcacea Lamarck 1809. This bivalve has been examined by Pelseneer (1911) and Heath (1941) but neither investigated the buttress or its functions. Thomas (1978: p. 188) commented upon the buttress of cucullaeids and noted that the posterior adductor muscle was attached to it. He did not, however, explain the significance of this.

Recently, a living specimen of *Cucullaea concamerata* was collected in Hong Kong; this study reports upon the function of the buttress in this species in relation to its life style.

## MATERIALS AND METHODS

On May 3rd 1980, a single pair of valves of *Cucullaea concamerata* was collected, using an Agassiz trawl, from about 8 m depth on a sandy bed containing large numbers of shell valves of



other bivalves including *Trisidos semitorta* (Lamarck), *Anadara antiquata* (Linnaeus) and *Tapes dorsatus* Lamarck. The station, situated in the north-eastern territorial waters of Hong Kong some 3 km to the east-south-east of the village of Sha Tau, in the People's Republic of China has the grid reference 225 994 (from 1:100,000. L681, 1970). On the 9th June, at the same station, a living specimen was obtained, similarly by Agassiz trawling.

The living specimen was dissected. Ciliary currents in the mantle cavity were determined by the application of carmine in sea water.

#### LIFE STYLE

The periostracum of both shells was heavily eroded posteriorly. In this region too the valves were extensively bored by the polychaete *Polydora* sp. This clearly suggests that *Cucullaea concamerata* lies buried in sublittoral sands, anterior end down, as shown in Figure 1. The valves

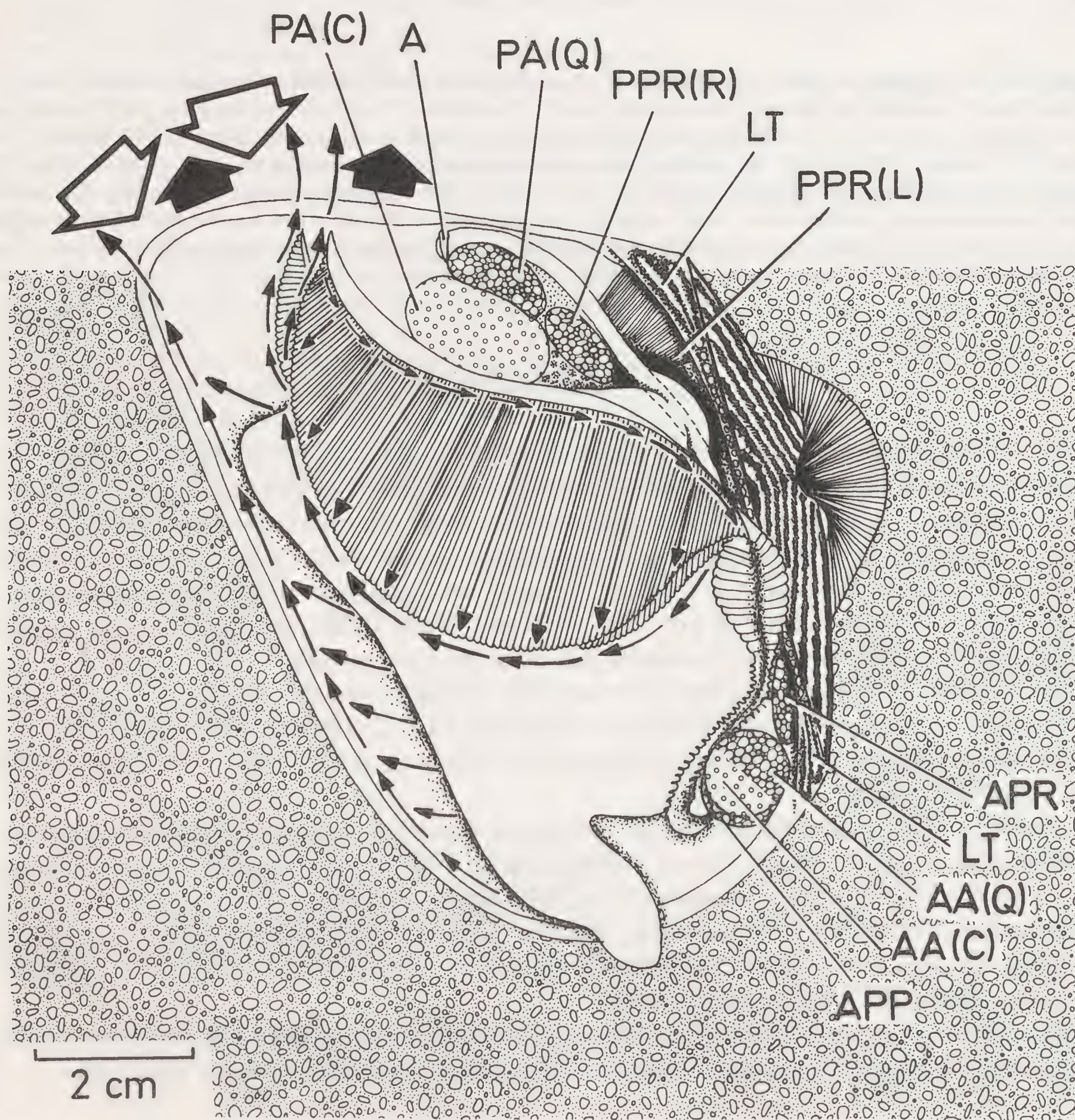


Fig. 1. *Cucullaea concamerata*. The organs of the mantle cavity after removal of the right shell valve and mantle lobe. The specimen is drawn in a natural position in the sand. Large open arrows represent the inhalant stream; large closed arrows the exhalant stream; small closed arrows the ciliary currents of the ctenidium and mantle. (For abbreviations see page 301).







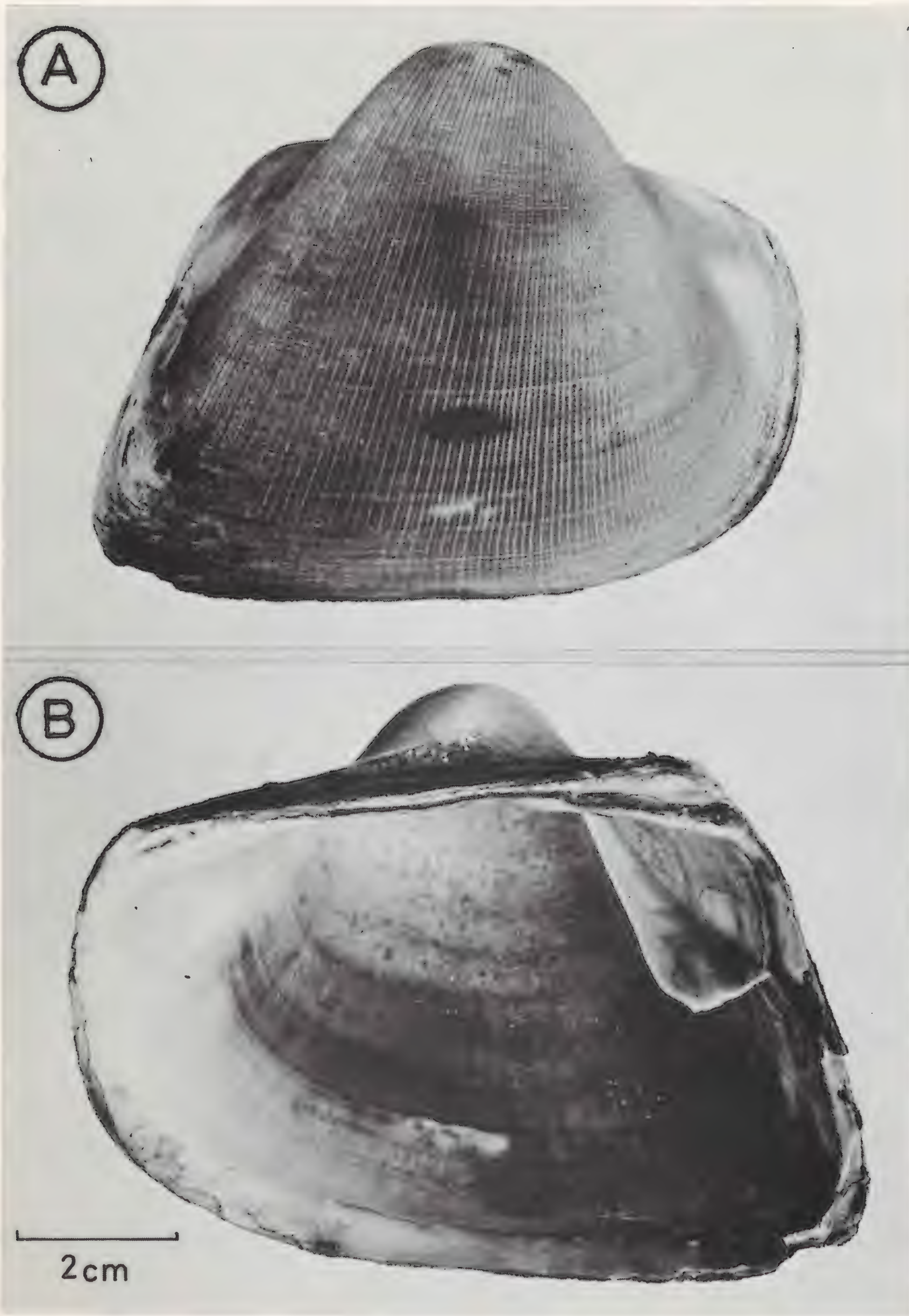


Plate 11. *CUCULLAEA CONCAMERATA*. EXTERNAL (A) AND INTERNAL (B) VIEWS OF THE RIGHT SHELL VALVE.



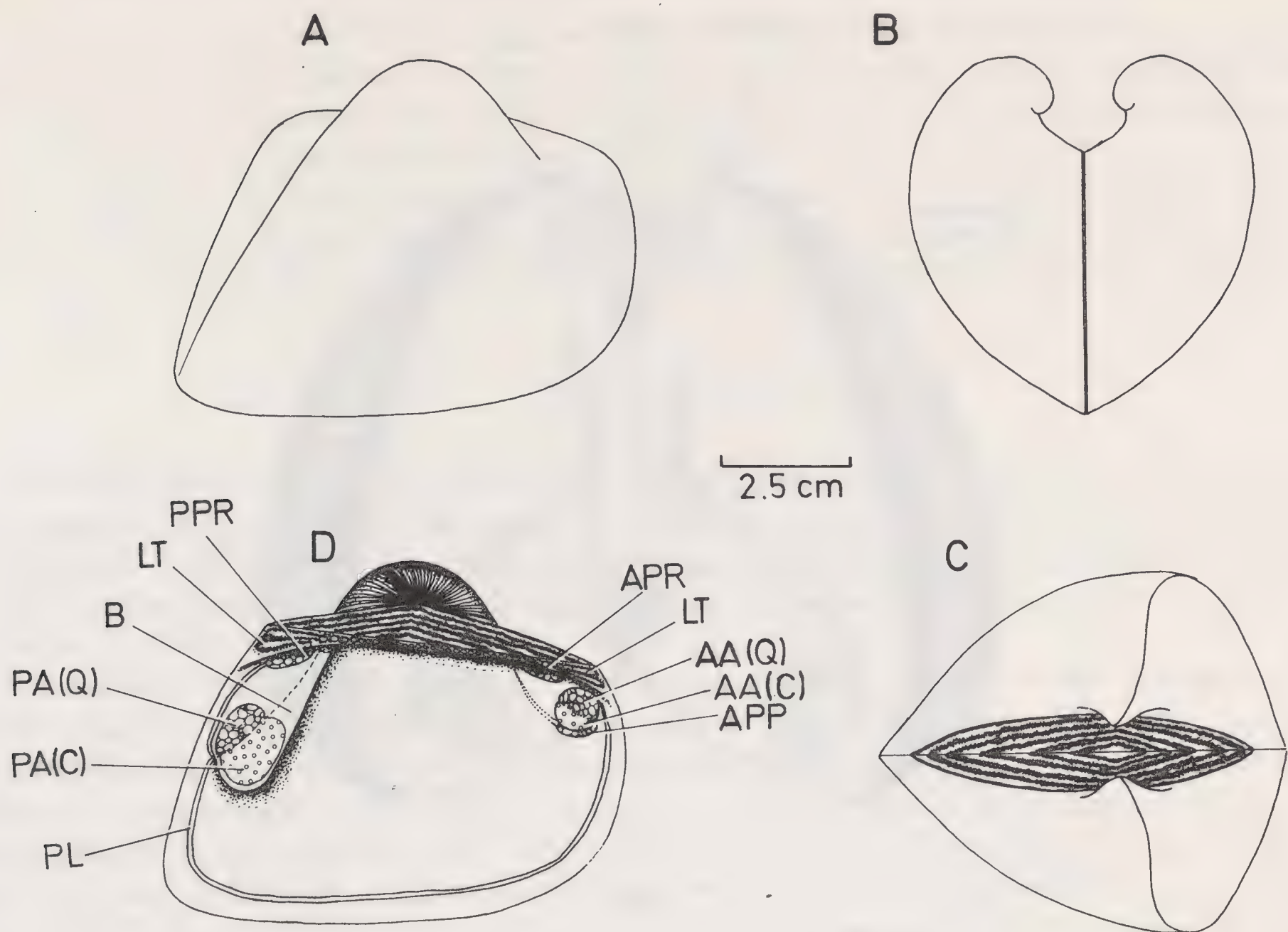


Fig. 2. *Cucullaea concamerata*. The outline of the shell as seen from (A), the right; (B), the posterior and (C), the dorsal aspects. (D), an internal view of the left shell valve showing the muscle scars. (For abbreviations see page 301).

of *C. concamerata* are strongly inflated (Fig. 2B) and the posterior face is antero-posteriorly flattened (Fig. 2A; C); this results in a shell that is somewhat truncate postero-ventrally, and rounded anteriorly (Plate 11A). The flattened posterior face of the shell thus lies flush with the sand surface or approximately so. Further evidence to suggest this is given by the direction of the rejectory currents of the mantle cavity (Fig. 1). Pseudofaeces derived from the tips of the posterior ends of the ctenidia (obtained from the rejectory tracts located in the ventral marginal grooves of both inner and outer demibranchs), and from the ciliary currents of the mantle are rejected postero-ventrally. In life, the shell valves gape widely, this being facilitated by the widely separate umbones (Fig. 2B). The posterior mantle margins are devoid of sensory papillae or tentacles. Thus although an anterior inhalant current is typical of the Arcacea (Lim, 1966), especially the nestling species, this is almost certainly not so in *C. concamerata*. Rather, an exchange of fluids with the waters above the clean sands this species inhabits is exclusively, and probably rather passively, via the posterior.

#### GENERAL FEATURES OF THE SHELL

As well as the general form of the shell earlier alluded to, a number of other features are important. The hinge plate and the taxodont teeth are very reduced, particularly in the central region. Laterally, however, two 'lateral teeth' (Figs. 1 and 2D, LT) are enlarged, those of the posterior region of the hinge plate being larger than those of the anterior. These teeth constitute the major locking mechanism of the shell, also being responsible for valve alignment. The teeth of the fossil *C. vulgaris* are altogether stronger (Thomas, 1978).

The anterior face of the shell is also generally reduced relative to the posterior so that the anterior adductor (Figs. 1, 2D and 3, AA) and pedal retractor muscle (APR) are smaller than



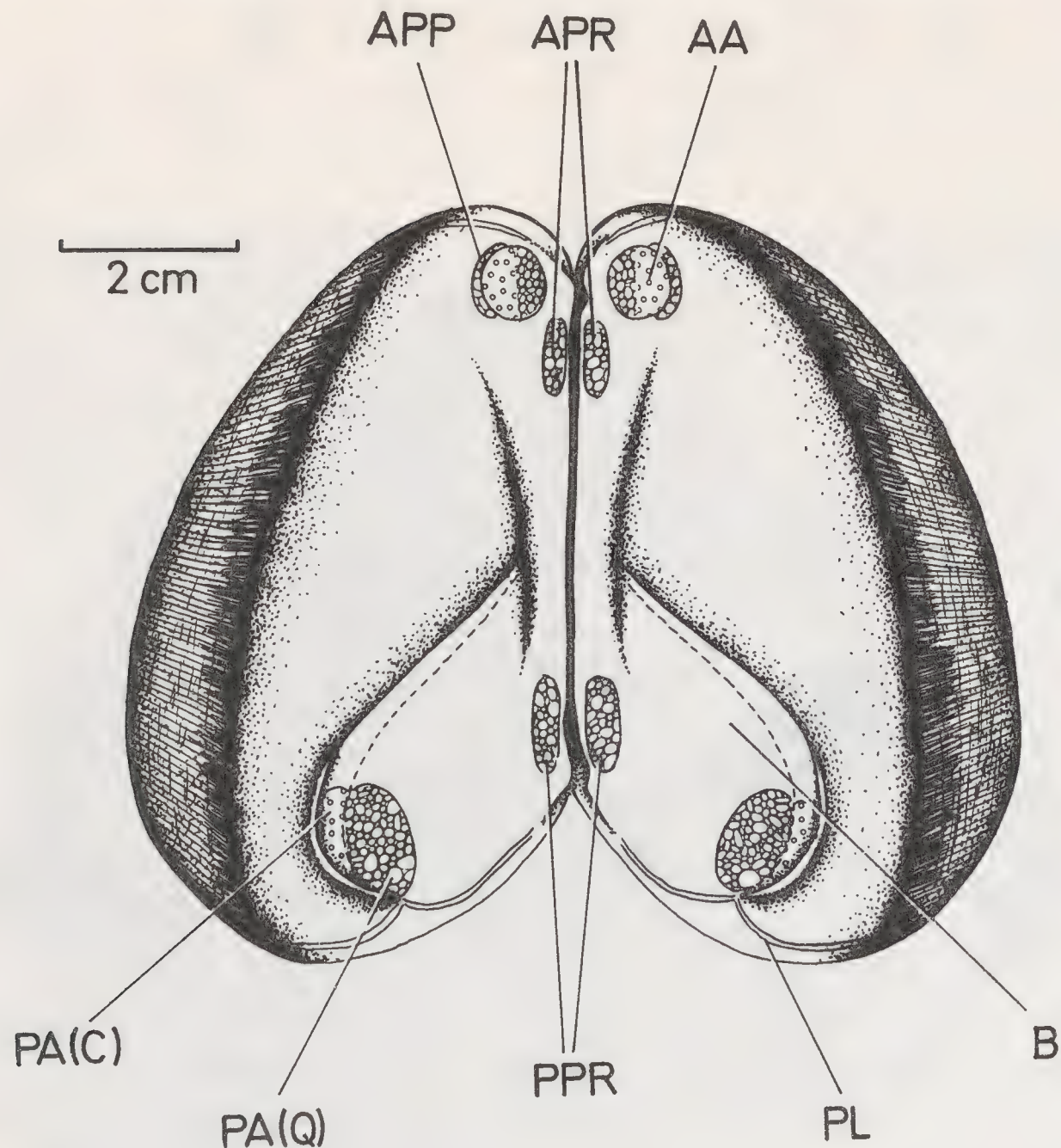


Fig. 3. *Cucullaea concamerata*. A ventral view of the inner surface of the shell showing the butresses and muscle scars. (For abbreviations see page 301).

their posterior counterparts (PA; PPR). Both adductors are aligned along approximately the same plane with regard to the ventral margin of the shell, but the posterior adductor muscle is more medially positioned, relative to the anterior adductor which is located just beneath the anterior lateral teeth. Anterior and posterior pedal retractor muscles are located on the dorsal border of the shell, separate from their equivalent adductors. The pallial line (PL) is thin, little muscularized and located close to the shell margin.

The most striking feature of the shell is, however, the butresses (Figs. 2D and 3; Plate 11B), one in each valve, and which arise internally from the umbones. Each comprises a relatively thick (not thin as indicated by Thomas, 1978) ridge, oriented at approximately right angles to the flattened posterior face of the shell.

#### GENERAL FEATURES OF THE MUSCULATURE AND ORGANS OF THE MANTLE CAVITY

When seen from the right side (Fig. 1), the visceral mass, containing gonad and digestive system, is large. The relatively small foot points anteriorly—it probably has little function as a digging tool. The ventral expanse of the foot possesses a long byssal groove and, according to Pelseneer (1911) a small byssus gland, though this is probably only functional in the juvenile. The foot possesses three major muscle blocks, the anterior and posterior pedal retractors (Fig. 3, APR; PPR) and the anterior pedal protractors (APP) the latter having their point of insertion ventral to the anterior adductor muscle. As noted earlier, the anterior adductor muscle is small and is approximately equally divided into 'quick' (striated) (AA(Q)) and 'slow' or 'catch' (smooth) (AA(C)), muscle blocks. The posterior adductor is at least twice as large as the anterior and is also divided into 'quick' and 'catch' components (PA(Q); PA(C)).



The heart is located anterior to the posterior pedal retractor. The ventricle is penetrated by the rectum which then passes between the posterior pedal retractor, over the posterior adductor to terminate on the postero-ventral face of this muscle in an anus (A). Thus, all waste products are discharged from the posterior region of the shell.

The posterior adductor muscle is attached to the buttress of the shell. Careful examination has revealed, however, that the 'quick' striated region of the muscle is attached to the valve itself and that it is largely the 'catch' (smooth) component which has its insertion on the buttress.

## DISCUSSION

In the Bivalvia, internal ribs strengthen the shell, especially in fragile-shelled, mobile species e.g. *Amusium* (Morton, 1980). In others e.g. members of the Lucinacea (Kauffman, 1967), the internal fold formed by the primary exterior sulcus marks the line of gill attachment and may be a platform for the gill muscles, or a buttress for gill support as well as attachment of the posterior adductor muscle.

A highly characteristic, well formed buttress is also seen in the members of the Periplomatidae but more obviously in species of *Laternula* of the Laternulidae (Morton, 1976). In *Laternula truncata*, contraction of the dorsally located anterior and posterior adductor muscles flexes the exceptionally thin shell at a transverse umbonal crack in each valve, the fulcra being the internal ligament and the mid ventral margin of the shell. The shell valves are emarginate anteriorly and posteriorly. As the shell flexes the resultant reaction of the forces acting upon it is not through the crack but is in a postero-ventral direction from the umbones (because the posterior adductor is larger than the anterior) and it is significant that this approximate line is marked by a thick ridge, the buttress. This confers strength upon this region of the shell under the greatest stress during valve closure.

In *Cucullaea concamerata*, a buttress is also seen, and though very similar in structure and orientation to that of *Laternula* has a very different function.

Unlike that of *Laternula*, the shell of *Cucullaea* is thick. Moreover, to the buttress is attached the smooth component of the posterior adductor muscle. The inflated shell of *Cucullaea* confers stability in a possibly unstable environment (Thomas, 1978). As well as being inflated, however, the posterior face of the shell is also antero-posteriorly flattened, this region lying flush with the sand—water interface. Inflation and posterior flattening has had two effects. First they have effectively increased the length, particularly, of the posterior adductor muscle and second increased the shear component of stress acting upon the attachment of this muscle. The least shear is created by a muscle acting at right angles to its attachment base. In the case of *Cucullaea*, the angle of shear would be (without a buttress) only  $10^\circ$  (from the horizontal) (Fig. 4). Significantly, the smaller 'quick' component of the posterior adductor is still attached to the general surface of the valve (as is the whole of the anterior adductor). This is probably because *Cucullaea*, like most arcids, with no siphons, does not have to actively produce strong phasic adductions to regularly exchange the water in the mantle cavity, but to the contrary lies relatively quiescent with valves widely parted, the inhalant and exhalant streams being produced by the ctenidial cilia. The slow component of the adductor muscle is, however, attached to the buttress, for obvious reasons. Generally it is this muscle component which tightly closes the shell valves when the animal is attacked. In such an instance, with no buttress, the effect of shear could be critical. The buttresses compensate this by first reducing the muscle length (thereby aiding valve alignment) and second by increasing the angle at which the adductor attaches to the shell, thereby improving the effective adhesion of the muscle to the shell (Fig. 4).

There is thus no functional similarity between the buttresses of *Laternula* and *Cucullaea*. Rather the buttress of *Cucullaea* should be compared with the myophore plate or septum of



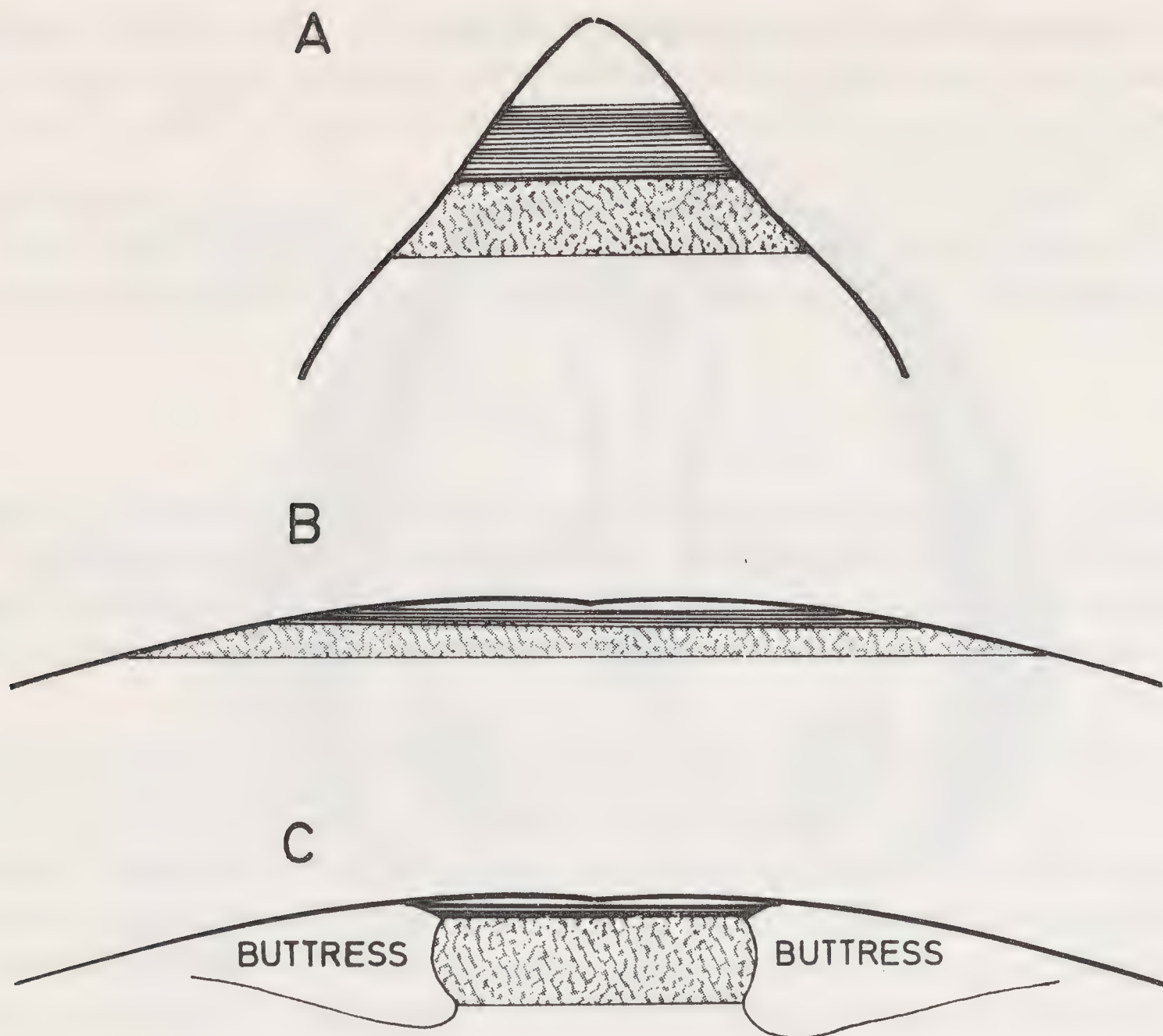


Fig. 4. *Cucullaea concamerata*. Diagrammatic representations of (A), the anterior region of the shell and anterior adductor muscle; (B), a hypothetical specimen with no buttress in the posterior region of the shell and (C), the effect of the buttress upon the disposition of the posterior adductor muscle. (Horizontal bars represent the 'quick' component of the adductor muscle, stippling the 'catch' component).

members of the Dreissenacea (Morton, 1969) (and possibly the mytilid *Septifer* (Yonge and Campbell, 1968)). In these byssally attached, heteromyarian bivalves, the antero-ventral region of the valves is flattened (a mechanism ensuring lateral stability in rapidly flowing waters) and the anterior adductor comes to be located on a septum, again to reduce the shear component of stress and to reduce the effective length of the muscle. In the genus *Mytilopsis* (Morton, 1981b), the anterior byssal retractor also comes to be located on a special lobe of the septum, again ensuring that contraction forces act at right angles to the attachment surface.

#### ACKNOWLEDGEMENT

I am grateful to Ms. S. Morris (British Museum (Natural History)) for confirming the identity of *Cucullaea concamerata* (Martini).

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#### ABBREVIATIONS USED IN THE FIGURES

|        |                                                            |
|--------|------------------------------------------------------------|
| A      | Anus                                                       |
| AA     | Anterior adductor muscle scar                              |
| AA(C)  | 'Catch' component of the anterior adductor muscle or scar  |
| AA(Q)  | 'Quick' component of the anterior adductor muscle or scar  |
| APP    | Anterior pedal protractor muscle or scar                   |
| APR    | Anterior pedal retractor muscle or scar                    |
| B      | Buttress                                                   |
| LT     | Lateral teeth                                              |
| PA(C)  | 'Catch' component of the posterior adductor muscle or scar |
| PA(Q)  | 'Quick' component of the posterior adductor muscle or scar |
| PL     | Pallial line                                               |
| PPR    | Posterior pedal retractor muscle or scar                   |
| PPR(L) | Left posterior pedal retractor muscle                      |
| PPR(R) | Right posterior pedal retractor muscle                     |







# NOTE ON THE IDENTITY OF *FISSURELLA* *IMPEDIMENTUM* COOKE, 1885 (PROSOBRANCHIA: FISSURELLIDAE)

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(Read before the Society, 13 December, 1980)

*Abstract:* The keyhole limpet, *Fissurella impedimentum* Cooke, from the Gulf of Suez, is poorly described in the literature. The syntypes of *F. impedimentum* are described and illustrated. Their preservation suggests that the form is from the raised shell beds of the Gulf of Suez. *Capulina ruppelli* var. *barroni* Newton is a junior synonym.

A keyhole limpet with an almost circular outline, brought back from the Gulf of Suez by Robert McAndrew, was described by Cooke (1885, p. 270) as *Fissurella impedimentum*. Unfortunately he did not add a figure of the new species and that is probably the reason why it has never been recorded again from the Red Sea. Also Christiaens (1974) in his review of the genus *Diodora* failed to mention it.

A study of the syntypes of *F. impedimentum*, present in the Mollusc Collection of the University Museum of Zoology, Cambridge, revealed that there are five specimens, instead of four as mentioned in the original description. They have the following dimensions: (mm)

| Specimen    | Height | Length | Width | Status                              |
|-------------|--------|--------|-------|-------------------------------------|
| UMZC 2354/3 | 9.5    | 10.8   | 10.5  | Lectotype (Plate 12, fig. 8)        |
| UMZC 2354/2 | 8.4    | 12.9   | 11.5  | Paralectotype (Plate 12, figs. 1-3) |
| UMZC 2354/5 | 7.5    | 9.9    | 8.8   | Paralectotype                       |
| UMZC 2354/1 | 6.7    | 10.4   | 8.2   | Paralectotype (Plate 12, figs. 4-5) |
| UMZC 2354/4 | 6.6    | 10.3   | 8.5   | Paralectotype (Plate 12, figs. 6-7) |

All show a radial sculpture consisting of 17 main ribs alternated with 3 less developed ribs, of which the one in the middle is the strongest, though, less developed than the main ribs.

Cooke did not mention a type locality in his description, while any indication concerning the origin of the material is also wanting on the original label. However, from the state of preservation of the shells, it is clear that we are most probably not dealing with a recent sample, but with material collected from the raised shell-beds which are found here and there along the Gulf of Suez.

As a matter of fact the shells are completely identical, except in size, with material described and figured by Newton (1900, p. 502, pl. 22, figs. 1-4) as *Capulina ruppelli* var. *barroni* from the raised beach deposits of Ras Gharib, Egypt. According to Newton his largest specimen measured: height 15 mm, length and width 18 mm.

Newton's remark is noteworthy: 'It is to be seen in an unnamed condition in the recent shell section of the British Museum, labelled as from the Red Sea, although the specimens have all the



appearance of coming from the beach deposits of that area. Probably the form is extinct.' I agree with his remark, however, I do not accept Newton's opinion that the specimens described by him belong to the form group of *Diodora ruppelli* (Sowerby, 1835). Size, height, circular outline and sculpture are so different that I consider it a good species, of which the following synonymy is now known:

*Diodora impedimenta* (Cooke, 1885)

*Fissurella impedimentum* Cooke, 1885: 270.

*Capulina ruppellii* var. *barroni* Newton, 1900: 502, pl. 22, figs. 1-4.

#### ACKNOWLEDGEMENT

I should like to thank Dr. C. B. Goodhart (Cambridge) for sending me on loan the type specimens of *Fissurella impedimentum* from the McAndrew collection.

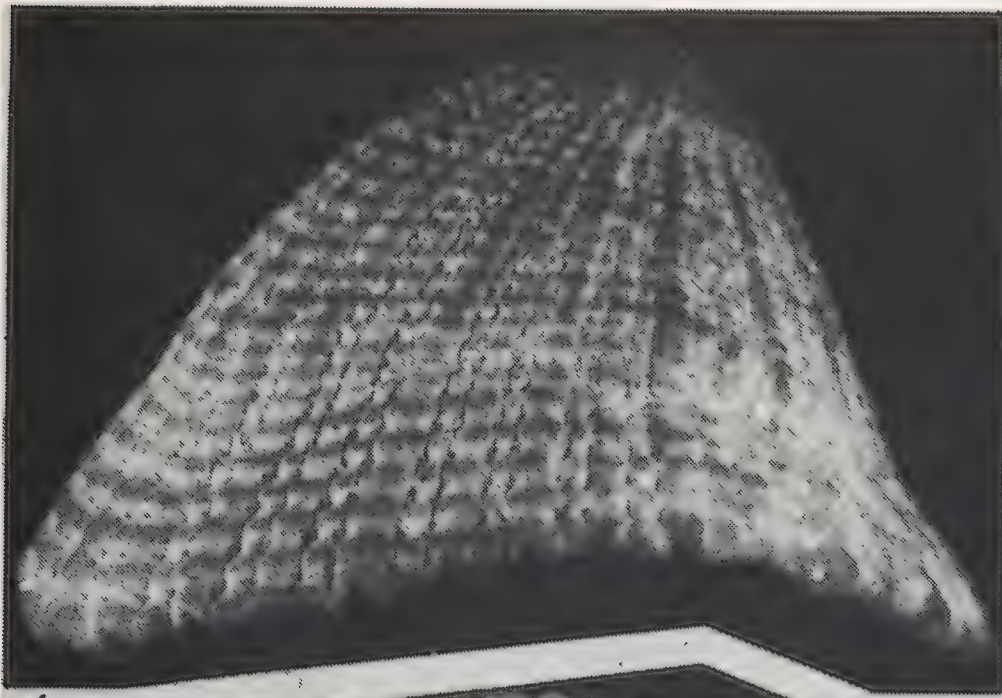
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#### PLATE 12 (opposite)

Syntypes of *Fissurella impedimentum* Cooke, Figs. 1-3, UMZC 2354/2; figs. 4-5, UMZC 2354/1; figs. 6-7, UMZC 2354/4; fig. 8, UMZC 2354/3. All × 5.





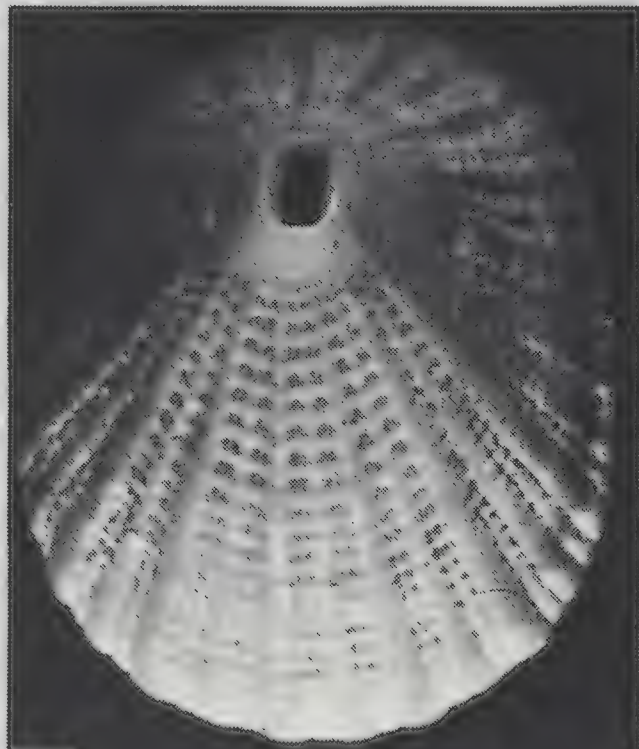
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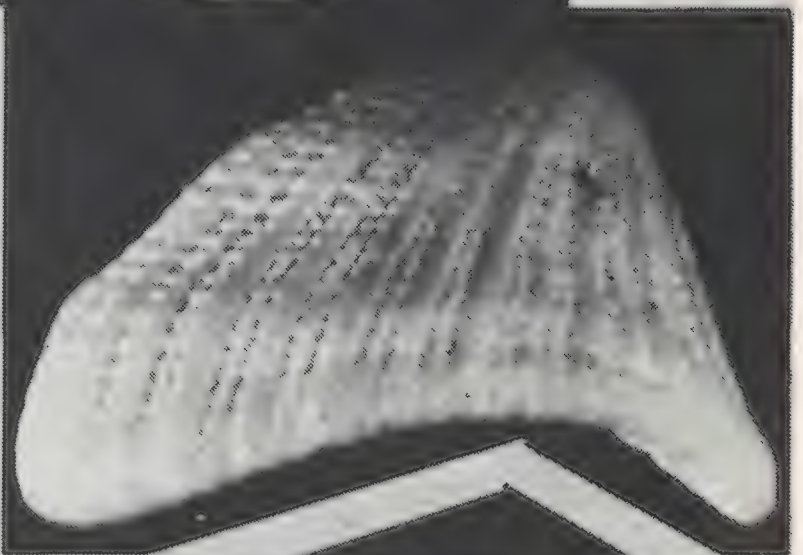
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# POSSIBLE ECOLOGICAL SIGNIFICANCE OF VARIATION IN SHAPE OF *CERION* SHELLS WITH AGE

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*Abstract:* European sand-dune pulmonate faunules show considerable variation between species in shape of shell, little during the lifetime of each. *Cerion* shows much variation in shape during the life-history but comprises in itself nearly all the coastal pulmonate faunule in the Caribbean. Comparison of its various shapes during growth with those of European species suggests that its different life-stages may occupy the niches of different European species.

It has been shown (Cain, 1977a, 1978) that the pulmonate faunas of widely different zoogeographical regions have, with only partial exceptions, the same bicuneate distribution of the values of shell height  $h$  and maximum diameter  $d$  for adult shells. Cain (1977a) suggested, and Cameron (1978) and Cain and Cowie (1978) have produced some confirmatory observations on the British fauna, that different shapes of shell predispose their carriers to walk on surfaces of different inclinations. This would allow these generalised feeders to reduce competition for food between forms with different shell shapes by feeding in different places.

European snails in general show little variation in shape of shell while growing up. Probably all are more or less globular when just hatched, whether by conformity to the shape of the egg or because the hatchling needs to be versatile in its walking, or both. Thereafter they soon approximate to the adult value of  $h/d$  and merely increase in size except for the formation of the lip, if any, and sometimes, as in large helicids, a slight change in axial direction of the last whorl just before the lip. One well-known exception in the helicids is *Theba pisana* in which the juvenile shell is much more flattened above, with a sharp angulation at the periphery, than is the adult shell which is subglobular with a well-rounded body whorl. The juvenile has been described as a separate species more than once (Taylor, 1912; Germain, 1929, 1930-31).

In contrast, many of the so-called species of *Cerion* show great variation in  $h/d$  during their life-history. A few unrelated species approach them in this respect; in Europe, for example, some orculids and pupillids (Kerney and Cameron 1979, pl. 2, Fig. 7a and b, and p. 93 text-figures A and B). The extreme species of *Cerion*, however, are nearly unique. The purpose of this paper is to compare their variation with that between species in a faunule of similar habitat, and to suggest a possible ecological explanation which would bring them into line with the hypothesis outlined above.

## VARIATION IN *CERION*

Adults in the genus *Cerion* vary from almost top-shaped through sub-cylindrical with a pointed apex to rounded-conical or almost teardrop-shaped like an enid. An excellent figure of





Fig. 1. Rough sketches of growth stages of *Cerion alberti* (top row, with two adults to show variation, after Clench and Aguayo, 1949) *C. geophilus* (middle, short row, after Clench and Aguayo, 1949) and *C. uva* (bottom row, from specimens in the British Museum (Natural History)). Also, adults of *C. hessei* (after Clench and Aguayo, 1949), *C. sculptum* and *C. tridentatum rocai* (both after Clench and Aguayo, 1953), group of three to right. Single adult at left, *C. stevensoni* (after Woodruff, 1978). Adults are roughly to the same scale, juveniles are somewhat enlarged for clarity.

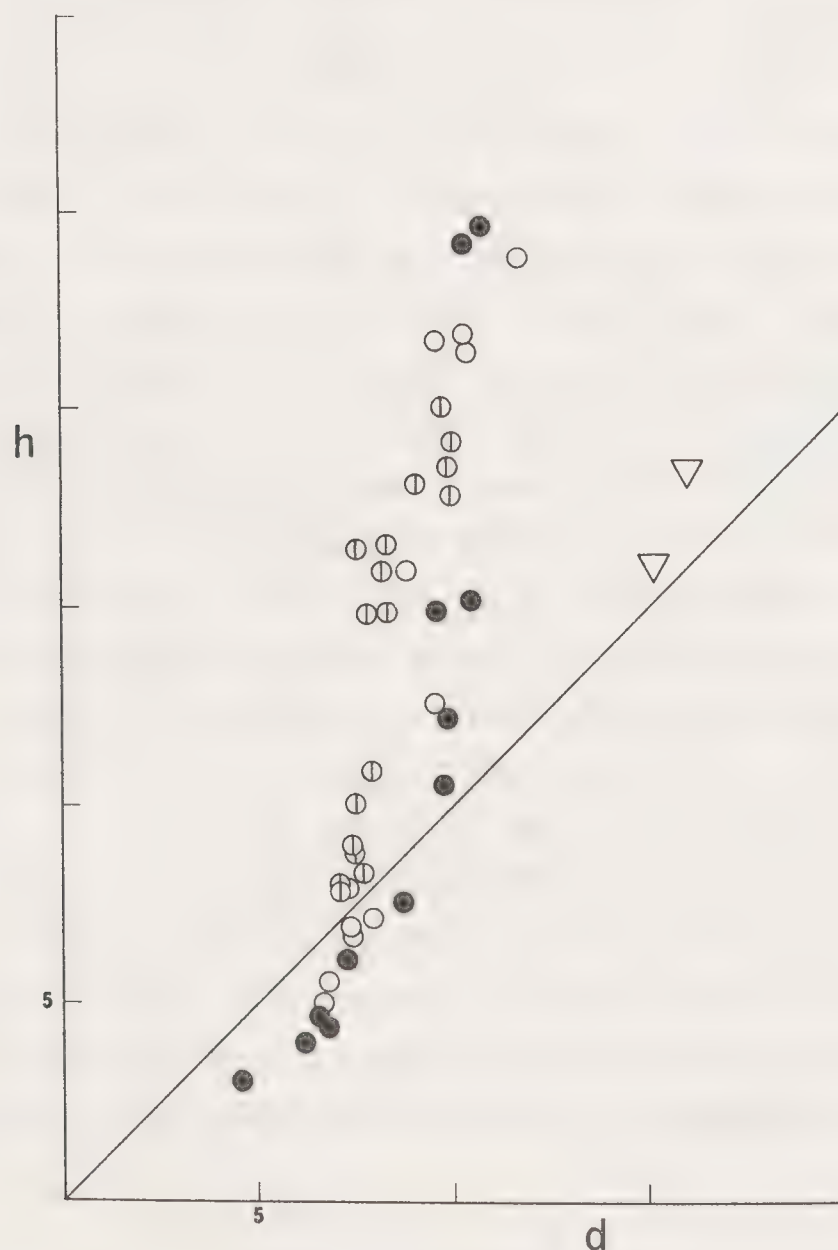


Fig. 2. Distribution of shell height  $h$  and maximum diameter  $d$  for growth stages of *C. uva* (black circles), *C. agrestinum* (white circles), and *martinianum caymanense* (circles with vertical line) from BM(NH) specimens, and for adults of *Hemitrochus varians* (inverted triangles) from measurements in Pilsbry, 1939. Axes marked at 5 mm intervals here and in subsequent  $h/d$  diagrams.



the variation in shape (and in size, ribbing, mottling, teeth and lip) is given by Gould, Woodruff and Martin (1974) and another by Woodruff in an important summary of knowledge of the genus and of work done on it (Woodruff, 1978). In all the so-called species that I have seen, inspection of the smooth nepionic shell suggests that it is subglobular, or rather flatter than that. In top-shaped species such as *Cerion alberti*, *C. geophilus* or *C. uva* (Fig. 1) the growing shell rapidly spreads out to become a very low cone, almost a disc, with a central knob formed by the nepionic shell. Further whorls are added without an increase in *d* so that the cone or disc now caps a column, which may decrease in diameter before the adult lip is formed. Woodruff (1978 p. 236) refers neatly to the three phases of 'juvenile triangularity, mid-growth "barrelling", and adult recurvature'. In Fig. 1 are shown growth stages illustrating these three phases in *C. uva* from a sequence in the British Museum (Natural History) originally put together by Canon Horsley. Comparable figures are given after Clench and Aguayo (1949) for *C. alberti* and *geophilus*. In addition to these species, the adults of less extreme forms are shown, namely *C. stevensoni* (enid-like) after Woodruff (1978), *C. hessei* (orculid-like), after Clench and Aguayo (1949), and *C. sculptum* and *C. tridentatum rocai* after Clench and Aguayo (1953). Usually only adult shells have been figured in the systematic literature; indeed, collectors have usually taken only adults, seldom even the larger juveniles. Small juveniles have been almost wholly neglected and were available to me only for *C. uva*. In Fig. 2 are given the data for *h* and *d* for the *uva* series and for less complete series of *C. agrestinum* and *C. martinianum caymanensis* also in the BM(NH).

*Cerion* is found on the coastal scrub vegetation in the Caribbean, some forms much further inland (see Woodruff, 1978, for a summary of its biology as known so far). In many localities it occurs in striking abundance, clinging to stems and shrubs in full sunshine. In this it resembles, as Woodruff notes (1978 p. 227), *Theba pisana* in the Mediterranean. In fact, such local abundance is characteristic of many dune species in Europe. *Cerion* is not uncommonly found by itself, but also occurs with *Hemitrochus varians* (D. S. Woodruff, personal communication). This is a far less conical snail, coming close to the bisector in Fig. 2, and approximating in appearance to an unusually conical form of *Cepaea*. Juveniles of it would sit very close to and below the bisector, probably hardly coinciding at all with any growth-stage of *Cerion*. *Cerion* appears to be longlived and slow-growing, taking three years to come to maturity (Woodruff 1978, p. 229), so that two or three growth-stages would normally be found in any population.

#### THE EUROPEAN SAND-DUNE FAUNULE

In striking contrast, on European sand-dunes a diversity of species is usually found. In the north-west of Scotland, vegetated shell-sand duneland is literally covered with enormous numbers of *Cochlicella acuta* and *Helicella itala*; in the north, *Cepaea hortensis* and even the near-marsh snail *Arianta arbustorum* may be common (Cain, Cameron and Parkin, 1969). In Ireland and on the coasts of Wales and England, *Cepaea nemoralis* is common, and locally *Helix aspersa*. Helicellines also abound – in Cornwall, for example, *Cernuella virgata* and *Candidula intersecta* may be as abundant locally as *Cochlicella acuta* or *Helicella itala*. In a few places in southwestern Britain and near Dublin, *Theba pisana* appears; further south in Brittany and on the north-western coasts of France, *Cepaea nemoralis* disappears from the dunes and *Theba* is the only medium-sized subglobular sand-dune snail. On Mediterranean coasts the large subglobular helicine *Eobania vermiculata* also appears (Bonavita and Bonavita, 1962); its ecological relations with *Helix aspersa* need investigation. A general survey of snails on Mediterranean and Atlantic dunes is given by Sacchi (1971).

Germain, in his study of the French non-marine molluscs (1930–31, p. 39) gives as a subdivision of his xerophil association a dune faunule which comprises '*Helicella* du groupe de l'*H. variabilis* Drap.', *Cernuella explanata*, *Trochoidea trochoides* (= *conica* and *crenulata*), *Cochlicella acuta*, *C. barbara* (= *ventricosa*) and *Theba pisana*. To these should be added, from his descriptions of their habitats, *Trochoidea pyramidata*, and *elegans*, and *Cochlicella conoidea*. The species



recognized by him in *Cernuella* include *C. variabilis* (= *virgata*) with var. *suberis*, *C. xalonica*, *C. maritima* with several varieties, and *C. ambielina*. All may be forms of *virgata*. No information is given about the relative ecological deployment of the different species of *Trochoidea*.

All Germain's species occur on the Mediterranean coasts of France and the Iberian coasts, some spreading up the Atlantic coast as far in a few cases as the British Isles (*C. virgata*, *C. acuta*, *T. pisana*). Only a few of all these species are confined, or nearly so, to the littoral habitats throughout their range – perhaps the most restricted are *T. pisana* and the genus *Cochlicella*, but *C. acuta* in Ireland, and *T. pisana* in Spain at least, are not confined to littoral habitats. On the French Mediterranean coast, *pisana* is not confined to sand-dunes (Bonavita and Bonavita, 1962). An apparant replacement, as one moves north, of *T. pisana* by *Cepaea nemoralis* and this latter by *C. hortensis* has already been referred to; probably there are similar replacements in the helicellines, especially in *Trochoidea*, but this subject needs further study. Subdivisions of the sand-dune faunule can no doubt be recognised, but for present purposes it is probably best to recognise only one faunule in western Europe, richly developed on Mediterranean coasts and attenuating (with replacement of species as well) northwards. Attenuation does not, however, reduce the range of values of  $h/d$ , the north Scottish dunes being inhabited by the depressed *H. itala* ( $h/d$  about 0.55), the subglobular *Cepaea hortensis* (about 0.8), and the high-spired *Cochlicella acuta* (about 2.5).

There is some difference from north to south in both colour and shape. While those species that habitually sit out in the sun have white shells with black bands in Britain as elsewhere, the occurrence of *Cepaea nemoralis*, *C. hortensis* and even *A. arbustorum* on British duneland imports into the faunule richly pigmented forms (bright yellow, pink, red, and dark brown) that are wholly absent further south. In extreme northwest Scotland even *Helicella itala*, which sits out, becomes dark-shelled, in correlation with the poor insolation (Cain, Cameron and Parkin, 1969). On the French Mediterranean coast near Montpellier, all the species have white opaque shells with, if any ornament, only thin black bands, lines or points, often confined to the lower half of the shell. Markings are often absent from the upper side, or only pale yellow is found as in the single band of *C. explanata*, seldom black. This change correlates well with the marked increase in insolation from north to south and is only a special case of a general rule of variation in land-snails (see Cain, 1977b).

In northwestern Europe all duneland snails have well-rounded whorls, those of *Cochlicella acuta* being the least ventricose (Fig. 3). In western Europe with the entry of *T. pisana* we find a strongly angulated shape in the juveniles only. (Germain (1930–31, p. 182) describes it as strongly keeled but sharply angulated is the better term). In southern Europe *T. pisana* is common and is joined by various species of *Trochoidea*, almost all of which are keeled, as is *Cernuella explanata*. The *Trochoidea* are conical, but *C. explanata* is flattened and like an exaggerated version of juvenile *pisana*. The significance of this apparent increase to the south of angulation and keeling is not clear. Almost all the west European species with strong keels are found in duneland, the only exceptions being *Helicigona lapicida* (widespread, often in rock-crevices), *Hygromia cinctella* (mainly southern) and *Ciliella ciliata* (alpine).

In Fig. 4 are given  $h$  and  $d$  values for adults of the French and western European duneland faunule, together with those for the rest of the fauna for comparison. The duneland-faunule species are medium-sized; neither small nor large (unless *H. aspersa* and *E. vermiculata* are included). They sample well the diversity in  $h/d$ , including the only genus, *Cochlicella*, to span the gap between the upper and lower distributions (the three black spots above the bisector). *Theba pisana*, *Trochoidea elegans* and *Cernuella virgata* are predominantly annuals in our breeding boxes, as are probably the rest of the species mentioned except those in the genera *Cepaea*, *Helix* and *Arianta*. Mr. R. H. Cowie tells me that at Tenby, *pisana* is biennial; in Israel it appears to be annual (Dr. J. Heller, pers. comm.). Since the juvenile stages, at least a whorl or so after the hatchlings, are similar to the adults, the symbol for each species will move approximately along a radius in the diagram towards the adult value each year. In Fig. 5 are given measurements for



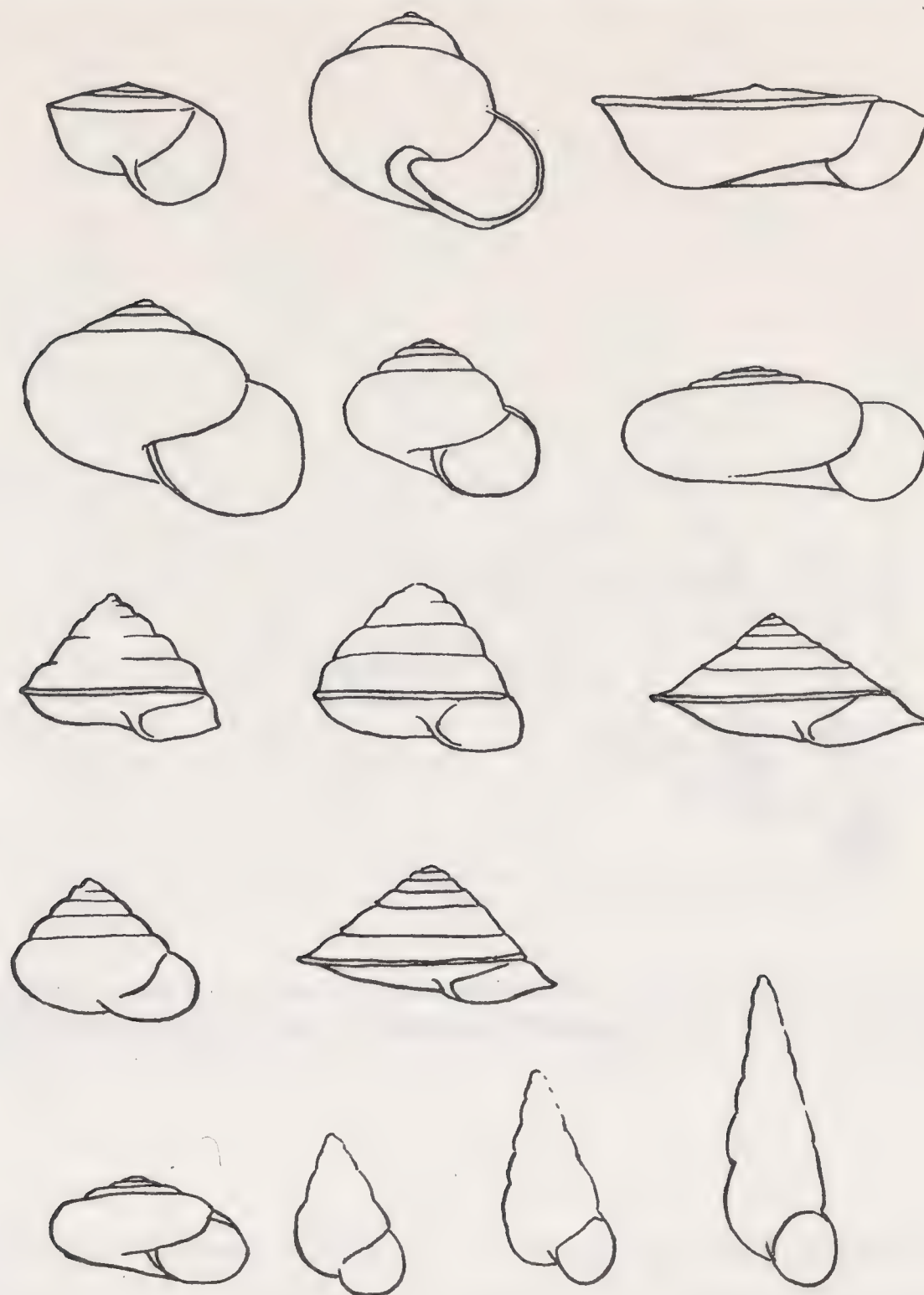


Fig. 3. Rough sketches of shell shapes of the sand-dune species given by Germain (1930–31) plus some for British dunes. Top row, juvenile *Theba pisana*, *Cepaea nemoralis* (British), *Cernuella explanata*. Second row, *Theba pisana* (adult), *Cernuella vigata*, *Helicella itala* (British). Third row, left and centre, *Trochoidea trochoides*; third row, right, *T. elegans* (form *scitula*). Fourth row, *T. pyramidata*, *T. elegans* (typical form). Bottom row, *Candidula intersecta* (British), *Cochlicella conoidea*, *C. barbara*, *C. acuta*. From my material or after Germain (1930–31), but with revised nomenclature.

juvenile and adult specimens of five of the species, and in Fig. 6,  $h/d$  is plotted against whorl number  $w$  for the same specimens. As already mentioned, most species are subglobular on hatching. Juveniles in *itala* and *explanata* seem to be not as flattened as the adults; *acuta* becomes more acute as it grows, as does to a much less degree *elegans*. Mr. R. H. Cowie informs me that both the very small juveniles and the subadults and adults of *pisana* are more globular than the intermediate stages. These changes in European species need further investigation; Fig. 6 shows, however, that they are slight compared with those in *Cerion uva* which goes through values of  $h/d$  from about 0.6 to 2.5. Fig. 4 shows that its life-track starts on a radius near that of *Cernuella explanata*, sweeps through that of (young) *T. pisana* and species of *Trochoidea*, and parallels and exceeds those of the genus *Cochlicella*. Fig. 6 compares this range in  $h/d$  against whorl number with those of some of the European species.

Since *Cerion* may take three years to mature, three different segments of this life track, or at least two, will normally appear on an  $h/d$  diagram for its faunule, whereas only one will be seen for many of the European snails. It is worth asking, therefore, whether the different stages of *Cerion* in the same faunule are occupying different niches corresponding to those of different species in the European faunule. Woodruff remarks (1978, pp. 226, 236) that the juveniles of most *Cerion* live on the soil surface under leaf-litter with the apex upward, whereas adults of most



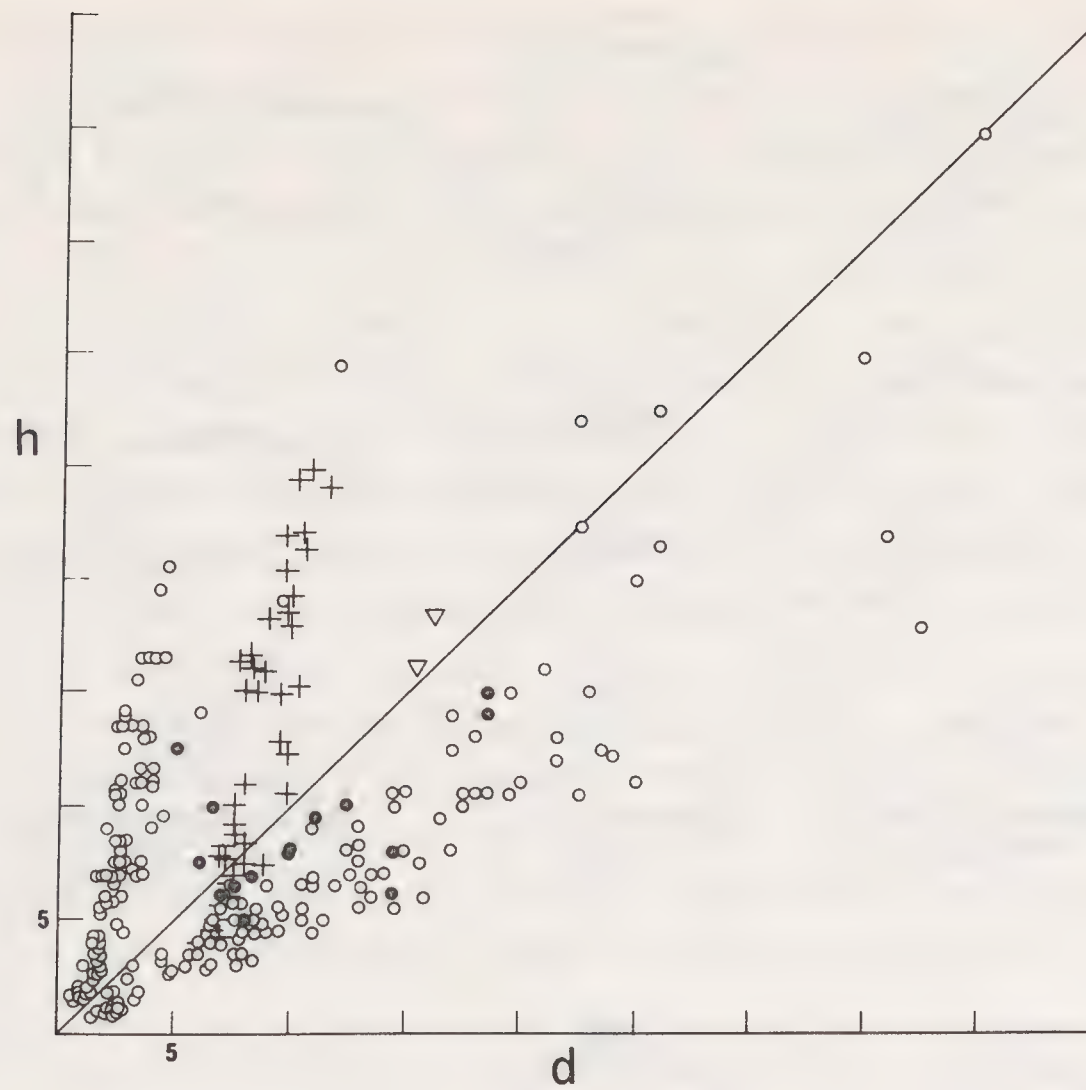


Fig. 4. Distribution of  $h$  and  $d$  for adults of the French land-snail fauna (data from Germain, 1930–31). Sand-dune species in black. For comparison, the growth stages of *Cerion uva* (crosses) and adults of *Hemistrochus varians* (inverted triangles) are added from Fig. 2.

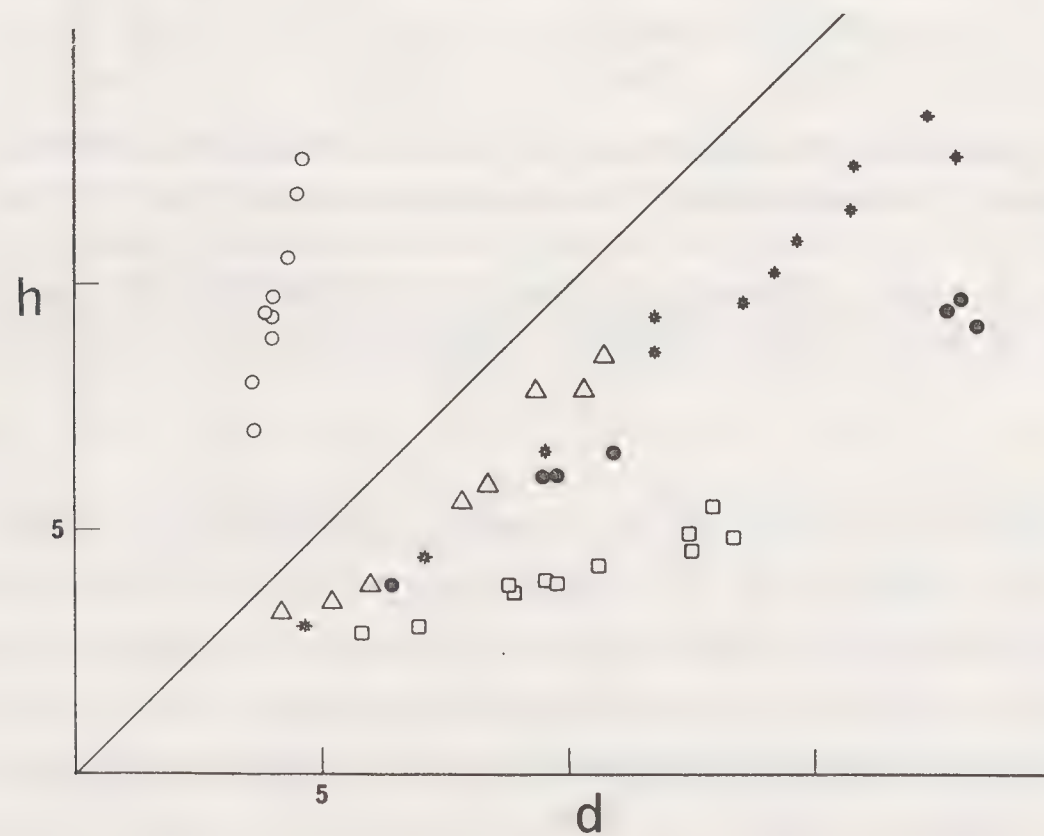


Fig. 5. Distributions of  $h$  and  $d$  for growth stages of some European sand-dune species. White circles, *Cochlicella acuta*; triangles, *Trochoidea elegans*; stars, *Theba pisana*; black circles, *Helicella itala*; squares, *Cernuella explanata*. From my material, but most specimens of *pisana* from R. H. Cowie's material from Tenby.



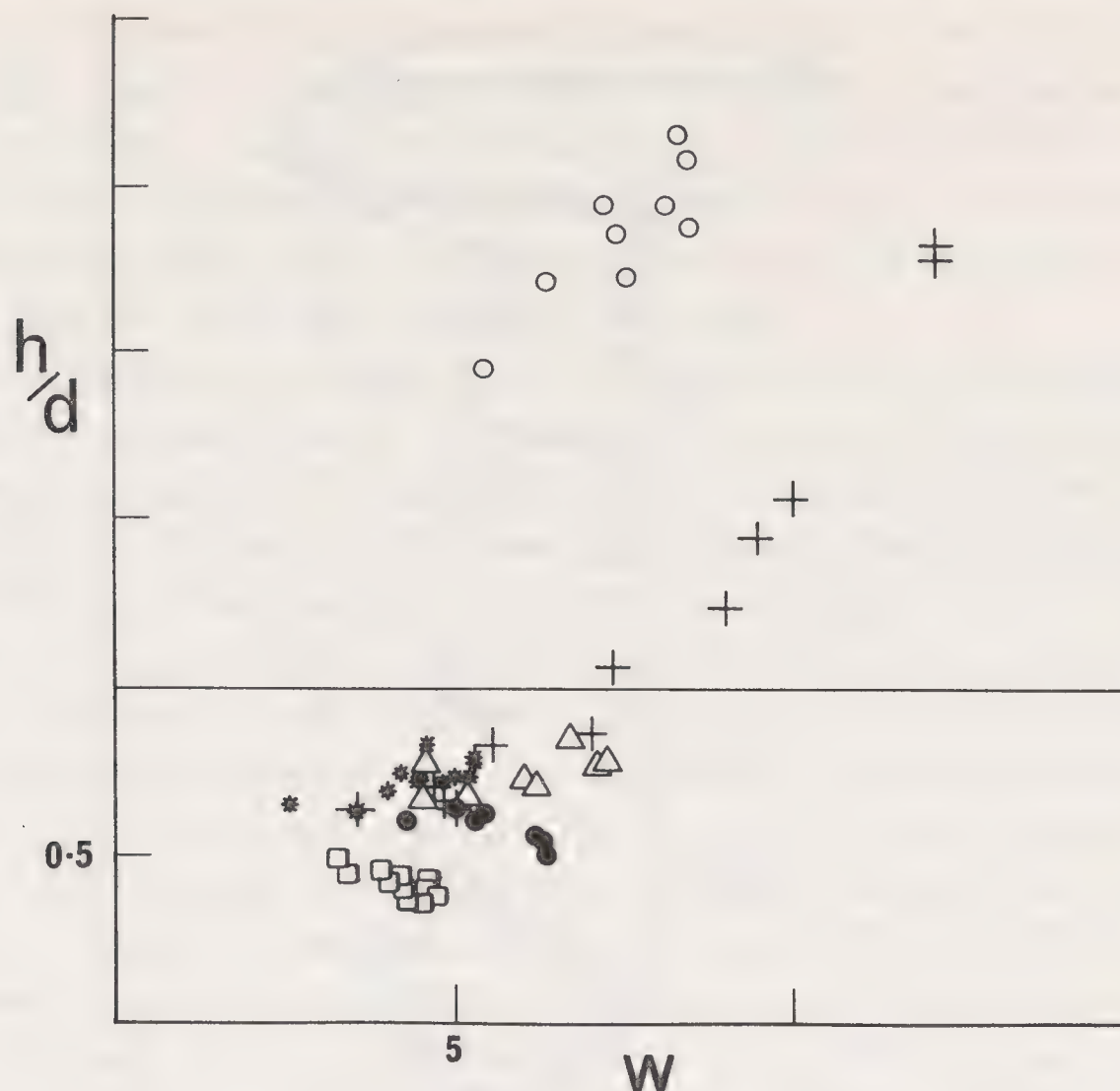


Fig. 6. Distributions of  $h/d$  against whorl number for the specimens shown in Fig. 5 (same symbols). Growth stages of *Cerion uva* (crosses) added from the specimens in Fig. 2 for comparison.

forms attach themselves to vegetation with the apex downwards during the day, moving about at night on the vegetation and on the ground (p. 277). Not even this much, unfortunately, appears to be known for the Mediterranean snails, so that until adequate investigations have been done, one must go by inference from the shell shapes and sizes.

#### DISCUSSION

*Cerion* resembles many of the species of the European sand-dune faunule in its coastal xerophil habitat, its local abundance, its habit of sitting out on stems and leaves in full sun, and its colour, white or mottled (with mottling cryptic, but plain white less liable to overheating, Gould and Woodruff, 1978 Fig. 4; Woodruff, 1978 p. 236). Juvenile stages (Fig 1) are highly reminiscent of juveniles, or even in some cases adults, of *T. pisana*, *C. explanata* and species of *Trochoidea* (Fig. 3). The range of values of  $h/d$  shown *within* the lifetime of more extreme species such as *C. uva* is not unlike that shown *between* adults of the European species, excluding the subglobular ones which, however, may be represented in the Caribbean by *Hemitrochus* (Fig. 4). Many of the smaller species of *Cerion* do not exceed in adult height *Cochlicella acuta*, but others go far beyond it. But by far the most obvious difference between *Cerion* and the European tall sand-dune species is that *Cerion* is almost always markedly fatter, and adults show no resemblance to any of the European species (compare Figs. 1 and 3). It might seem rash to suggest that, say, an adult *C. uva* on Curaçao is fulfilling the same ecological function as a *Cochlicella acuta* in Cornwall.

Certainly, the displacement of later juvenile stages of *C. uva* to the right of the species of *Cochlicella* (Fig. 4, the black circles above the bisector) is statistically significant – they and the *Cochlicella* species cannot be two random samples drawn from the same population. Nevertheless, they may not be different ecologically, but diverge in another way. Since the various European species have independent life-histories, each can specialise in its niche with only ecological pressure from those other species that coexist with it. But a species that begins as



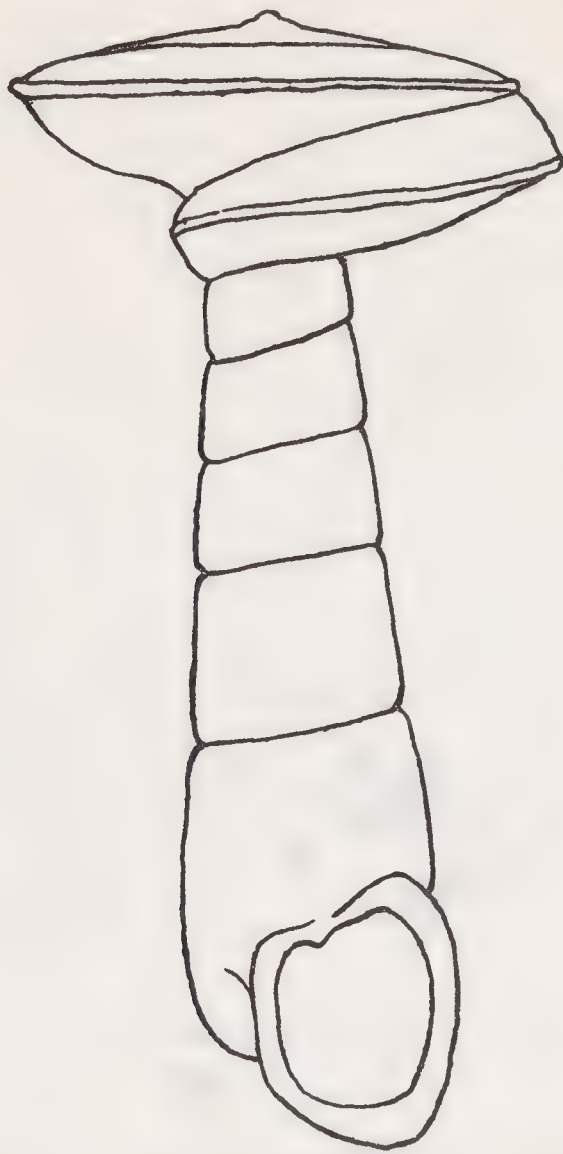


Fig. 7. A shell shape not known to have been evolved by *Cerion*, nor indeed by any other gastropod.

a disc and goes on to elongate must (unless it decollates which *Cerion* does not) add on increments to its shell which are mechanically integrated with preceding ones. No gastropod shell that I know of starts as wide as a young *pisana* and then changes abruptly to the narrow column of an *acuta* (Fig. 7). Such a shell would be impossible to burrow with or even to drag through leaf litter, which it would accumulate like a garden rake. Its weight would be concentrated at the end farthest from the animal's foot like the bob of a pendulum, giving the shell maximum instability and requiring maximum expenditure of energy to hold it in any given position. It would also be liable to break across at the junction between the disc and the rod. A species such as *Cerion uva* may well be under a constraint from the form of its juvenile shell to elongate without diminishing its diameter suddenly, although it and some other species do decrease their diameters slightly – even if only on the body whorl, e.g. *Cerion sculptum* (Fig. 1). 'Constraints' have suddenly become fashionable (Gould and Lewontin, 1979) for explaining away (see Cain, 1977c) structures which on a superficial view have no obvious function, and have not been properly investigated; nevertheless, the concept can be a useful one if the appropriate work is done to validate its use.

The high number of whorls in adult *C. uva* and many other *Cerion* species may perhaps support the suggestion just given. The relationships between whorl number,  $h$ ,  $d$ , and  $h/d$  in some land-snail faunas have been investigated by Cain (1980). In general, tall slender shells increase in height by adding large numbers of whorls, tall medium ones by adding much fewer, and tall fat ones such as succineids by adding very few. For a rather fat shell, *Cerion* has a markedly high whorl number. For the Floridan endemic (and only) species, *C. incanum*, values of  $h = 31.0$  mm,  $d = 10.5$  mm,  $h/d = 2.95$  and  $w = 12$  (from Pilsbry, 1946) were used in Cain's figure 15, 16 and 17 (Cain, 1980). These figures show that this species has an unusually high value of  $w$  for its  $h/d$  ratio; comparison of Cain's figures 6, 12 and 23 (European fauna, California and Arizona fauna, and Javanese fauna) with his Fig. 17 (Floridan fauna) suggests that  $w$  for this species should be 6 or 7, not 12. Specimens of *C. uva* with a lower  $h/d$  ratio ( $h = 24.4$ ,  $d = 10.5$ ,  $h/d$  only 2.3) also have 12 whorls. Cain (1980, p. 214) thought that *C. incanum*, although peripheral to the general distribution of  $h/d$  against  $w$ , probably did belong to it; his



figures 15, 16 and 17, however, show it as exceptional within its own fauna and other species of *Cerion* would be within theirs. The effect of increasing whorl number is to provide a greater degree of internal strutting, making the shell stronger against mechanical deformation; this again suggests (but does not prove) that the adult shell of at any rate some species of *Cerion* is a rather improvised construction, requiring more than the usual structural elements to combine the breadth of the juvenile with the height of the adult.

But why should *Cerion* have the opportunity (if indeed it does) to constitute in itself so large a part of the Caribbean coastal fauna? At present the genus comprises four subgenera (one extinct), fifteen species-groups and about 600 nominal species but there is very little sympatry (Woodruff 1978, pp. 224–5). Nearly all the nominal species are spatially separate populations or intergrade smoothly with their neighbours. Probably not more than 20% are valid (Woodruff 1978, p. 224). Effectively, in nearly every locality there is only one species. Moreover, the distribution in the Caribbean is extraordinary – the Greater Antilles; the Bahamas; the Florida Keys and nearby (one endemic species); and the Dutch Leeward Islands (Curaçao, Aruba, Bonaire, with again a single and endemic species, *C. uva*). There are none in Jamaica (although there are in the Cayman Islands) nor in the Lesser Antilles. The plate tectonics of the Caribbean and Central America is a highly complex subject (see e.g. Seyfert and Sirkin, 1973, pp. 327, 356, 389) probably involving several small plates or fragments. Vulcanism was widespread in the Greater Antilles in the early Tertiary, but stopped in the middle Eocene, about when it began in the Lesser Antilles which have a very different Tertiary history; either the same plate changed direction in the middle Eocene, or different plates were involved. While the Mediterranean has had a troubled history in the Tertiary, even drying out completely (Hsü, 1972), the Atlantic shores of Europe have been much less disturbed, and probably could have retained a sand-dune faunule in some completeness. It is possible that earlier (Mesozoic?) shores in what is now the Caribbean had so troubled a history that at some period, not necessarily the same everywhere, abrupt submergences or emergences destroyed the coastal vegetation completely and with them whatever faunule they possessed. Vertical movements of only a hundred feet or so would be quite enough to flood or wash down loose soils, since volcanic islands usually have steep sides. On their subsequent re-establishment, the vegetation of the new coasts would offer a chance to tough species, probably living on exposed rock, to invade them in spite of the exposure, heat, and saline spray. Only two stocks, *Cerion* and *Hemitrochus*, did so, and *Cerion*, if its immediate ancestor was a tall fattish shell, was preadapted to take up several niches, whereas *Hemitrochus* was not. Later, after the resulting faunule had spread widely in the Caribbean, differential uplifts or submergences removed them from the Lesser Antilles, and from Jamaica (if they had ever reached it). This suggestion seems more likely than the usual explanation, rightly rejected by Woodruff (1978), that the distribution of *Cerion* has been influenced on a major scale by hurricanes. Such a course of events would suggest that the inland species of *Cerion* are secondary, spreading from the coast where ecological opportunity allows.

There is, however, one qualification which must be made to this hypothetical history – although there is a species-rich sand-dune faunule on western and southern European shores, it is not of species confined to that habitat. As already mentioned, hardly one of the species concerned is confined to littoral habitats in general, still less to actual sand-dunes, and most are widespread in a variety of habitats in some part of Europe at least. A few possible exceptions in *Trochoidea* and *Cernuella* need investigating in North Africa, where they too may be more widespread. Conversely, there are species which live on rocks in full sunshine on the coast in salt-sprayed vegetational zones but which do not appear on duneland. Bonavita and Bonavita (1962) give *Sphincterochila candidissima* as on maritime rocks. This species sits out in full sunlight (Germain, 1930–31) but is not recorded, so far as I know, from duneland. Its congeners extend from summer-dry to actual desert conditions in the eastern Mediterranean countries, but are also not duneland forms. Exactly what it is that qualifies a species for living on duneland is not clear – it may well be the ability of egg-clutches or hatchlings to resist dessication or of eggs to



hatch rapidly so that they are not likely to be caught by a spell of dry weather, as well as the ability of the juveniles and adults to withstand insolation, and salt spray.

If the European duneland faunule is, equally with the Caribbean coastal faunule, of opportunist species, then its diversity of species that have been able to colonise the habitats needs explaining. Certainly, such forms as *Cepaea hortensis* and *Arianta arbustorum* come only on to cool wet duneland having an extreme Atlantic climate as is evident by the shell colour as well as by the known climates of north-western Europe. Some species of *Trochoidea*, and perhaps *Cochlicella* and *T. pisana*, may be genuine sand-dune species, only migrating inland where conditions are comparable. Probably the European faunule is composite, with a true sand-dune element plus a number of adventives assisted by the peculiar climate of western Europe to colonise what would otherwise be too extreme a habitat. The lack of an abundant sand-dune faunule in eastern North America may well be due to the comparatively extreme conditions in summer (or both summer and winter in the north) and the consequent difficulty of recruiting from an almost entirely woodland faunule. Unfortunately, sand-dunes are unlikely to produce a good fossil record.

If all these suggestions concerning *Cerion* are right, it still remains to explain its extraordinary variation in shell shape, sculpture and colouring from place to place. *Cerion* certainly undergoes predation. Ribbing may be related to its intensity and colour should be related to the degree of insolation (Woodruff, 1978), no doubt in connection with the amount of shading provided by the vegetation locally. The occurrence of a small clump of bushes on Mediterranean dunes clearly has had an effect on the faunule, some species actually avoiding the shade and others preferring it. Different vegetations may well provide, with very strong local differences, different proportions of available niches—for example, if the only exposed horizontal surface is pure sand, arid, barren and extremely hot, the niche for disc-like juveniles may be absent; if the ground is covered by a permanent layer of leaf-litter, it may be capacious. All these suggestions can be tested by field-work, which is now needed on both Caribbean and European shores throughout the year.

#### ACKNOWLEDGEMENTS

I am specially indebted to Professors S. J. Gould and D. S. Woodruff for personal information and encouragement to speculate about *Cerion*, and to the latter for criticism of this paper; to Mr. R. H. Cowie for the loan of specimens and for much information on the ecology of *Theba pisana*; and to him, Professor J. D. Currey, Dr. R. A. D. Cameron and Dr. L. M. Cook also for criticism; to Professor G. Valdeyron for a tour of habitats including dunes near Montpellier; and to Dr. P. B. Mordan for his willing permission for me to work on the collections of the British Museum (Natural History).

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# DIFFERENTIATION OF THE RADULA OF SOUTH AFRICAN SPECIES OF THE GENUS *GULELLA* INTO THREE TYPES (GASTROPODA PULMONATA: STREPTAXIDAE)

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(Read before the Society, 18 October, 1980)

*Abstract:* Radula studies of South African species of the streptaxid genus *Gulella* have revealed that among the 48 species examined three basic types of lateral tooth structure may be distinguished in addition to a fourth type different from all the others (*Gulella browni*). The various types are described and illustrated.

## INTRODUCTION

Published studies of the genus *Gulella* in Southern Africa (Connolly, 1939; 18-97, is still the only comprehensive account, although now out of date) supply little detail as regards the radula (literature references under the species in Connolly, op. cit., indicated with R); one illustration (p. 85) shows only a generalized tooth structure. The genus is widely distributed in Africa and the literature containing radula data is scattered over a host of papers not directly available to the present author. The findings presented in this paper are the result of observations made over a period of eight years, covering 48 species and describe and illustrate three basic types of lateral tooth structure and a fourth type remarkably different from other species of the genus studied by the author.

## MATERIALS AND METHODS

Specimens were obtained from 48 adult specimens of *Gulella* collected mainly by Dr. H. E. van Hoepen in three of the four provinces of the Republic of South Africa, the Transvaal, Natal and the Cape Province, in the period 1971 to 1979.

Because of the diminutive size of the majority of the shells, the following method of extraction and mounting was employed. After the specimen was identified the animal was relaxed by immersing the whole shell in tap water for 24 hours and, when the animal was extended, it was killed by immersing in a 70% ethyl alcohol solution. Subsequent boiling of the shell plus animal in a 5% potassium hydroxide solution usually resulted in obtaining an easily mountable radula which was cleared of KOH by boiling in distilled water. Even when the animal failed to emerge from the shell, the whole shell was boiled in the KOH solution and any air bubbles trapped between the retracted animal and the aperture of the shell were driven out as the temperature approached boiling point. On cooling the caustic solution was drawn into the shell and began to dissolve the tissues. Repeated boiling and cooling resulted in the complete dissolving of the tissues and the release of the radula without harm to the shell except for removal of the periostracum when present. However, the sculptural details of the shell are accentuated by this treatment.



Staining proceeded as follows. While still water-wet, the radula was immersed for one minute in Shirlastain 'A' (a differential textile dye made by the Shirley Institute, Manchester, England). This has the effect of staining the nascent teeth red and the more mature teeth in shades of purple and blue, clearly delineating the cusp from the base and the basal membrane. In some specimens the teeth were stained red throughout and the base blue. The composition of the various parts of the teeth and the reason for their acceptance of the different colours of the dye is not known to the author. After staining the excess was removed with a distilled water rinse and the radula transferred direct to a slide and mounted in a poly-vinyl-alcohol/phenol/lactic acid mountant, thus avoiding the necessity of dehydration.

The composition of the mountant is as follows:

- |                                      |                  |
|--------------------------------------|------------------|
| 1. distilled water                   | 34 parts by mass |
| 2. lactic acid, pure                 | 22 parts by mass |
| 3. reagent grade phenol              | 22 parts by mass |
| 4. low viscosity poly-vinyl alcohol* | 22 parts by mass |

\* (Rhodoviol 4-125 ex Rhone Poulenc, Paris, or  
Moviol 4-88 ex Hoechst, Frankfurt)

Mix 1, 2 and 3 and stir to a clear solution, add 4 and stir until dissolved. A water bath at 60°C facilitates solution.

Slides mounted by the above method are still in satisfactory condition after ten years. However, one of the drawbacks of this mountant is its very acidic nature which tends to leach out some of the red component of the Shirlastain. Other, more neutral mountants have been tried and the best of these has been Farrant's Medium which has excellent colour retention but tends to develop air bubbles in all but the thinnest mounts and it is also difficult to obtain gum acacia solutions at high solids completely free of extraneous matter. The method has been given in some detail because of the effectiveness of the extraction procedure and the importance of the differential stain, without which the finer features of the tooth structure do not become apparent.

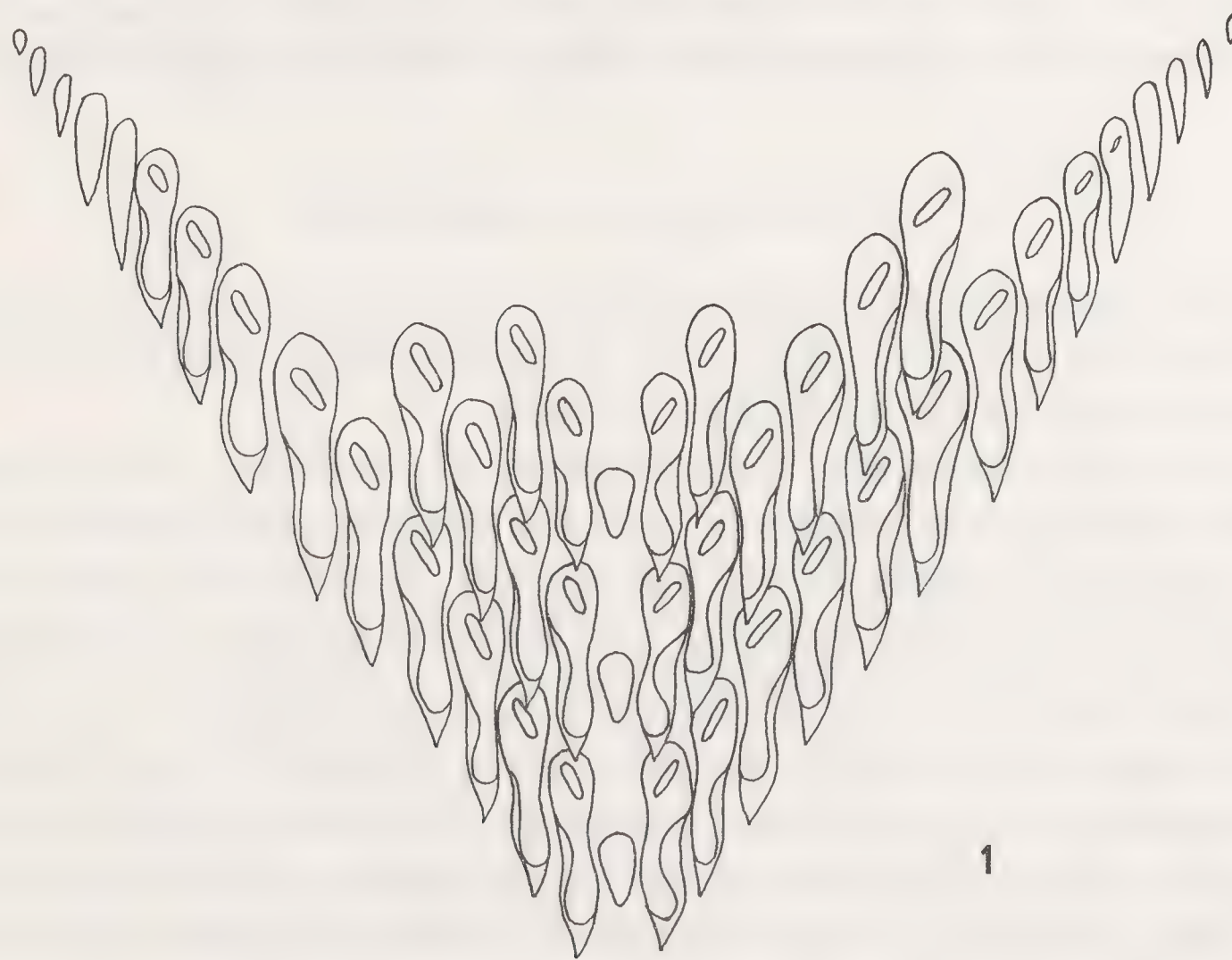


Fig. 1. Part of radula of *Gulella barnardi* Van Bruggen. Scale 0.1 mm.



Of course, radulae may also be prepared following the various classical methods with Canada balsam, glycerine jelly, etc., which give good results with comparatively simple procedures.

## OBSERVATIONS

The radula in the genus *Gulella* consists of numerous rows (from 50 to 250 ) of teeth with a unicuspid central tooth and unicuspid lateral teeth numbering from 8 to 50 on either side of the central tooth. Occasionally the central tooth is absent. Fig. 1 illustrates the general arrangement of the teeth on a radula and, during the first few years of collecting, all those examined appeared to be remarkably similar. However, as more material became available, it was possible to separate the species into three basic types based on the structure of the lateral teeth. The following outlines the differences observed.

## TYPE 'A' (Fig. 2)

This is by far the most numerous type and has lateral teeth that have an area of basal attachment greater than the free cutting point. In addition there is a process on the base, set at

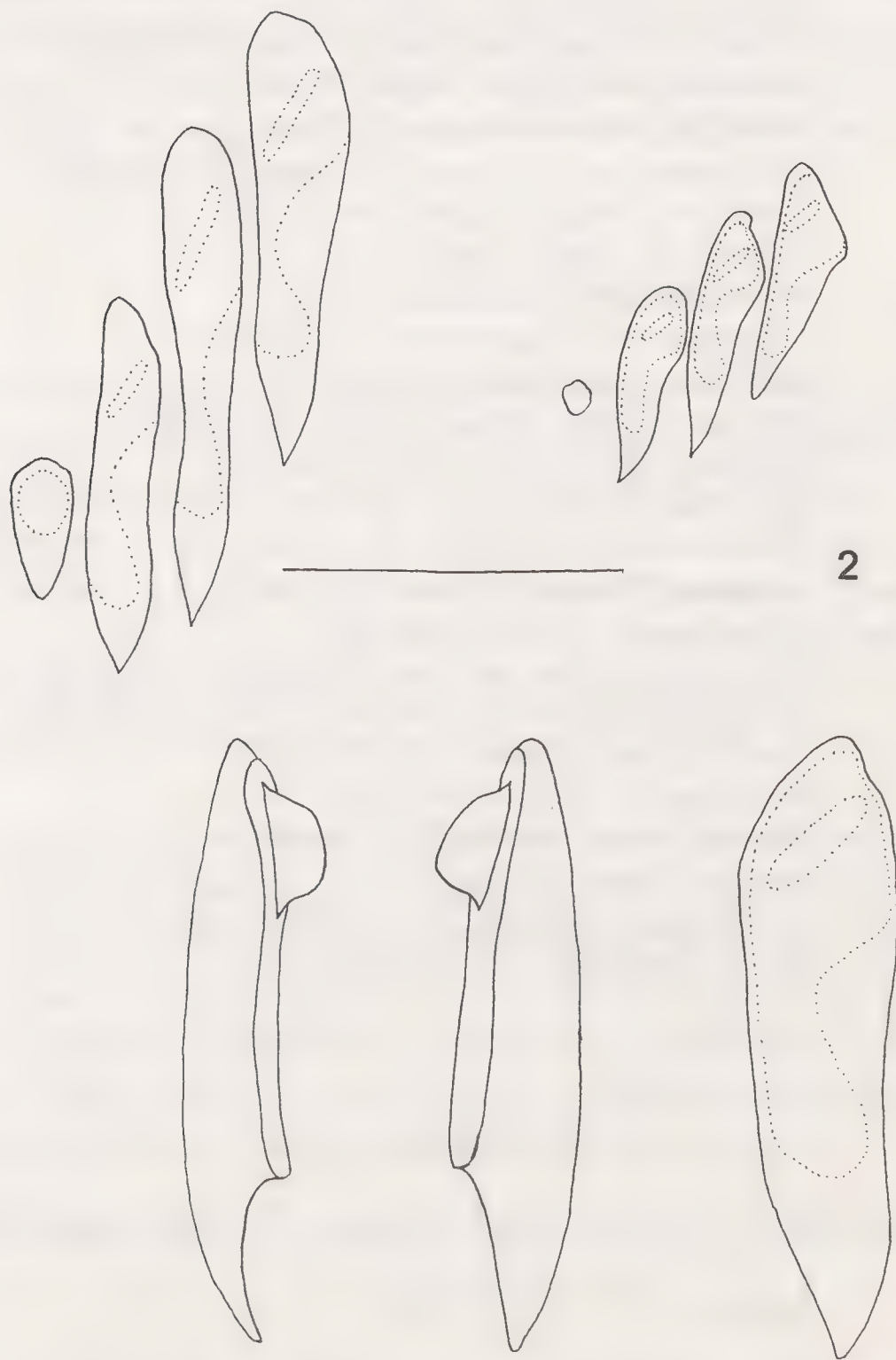


Fig. 2. Radula type 'A' of *Gulella*, upper left *G. gouldi* (Pfr.), upper right *G. infans* (Crvn). Scale 0.05 mm. The central tooth is shown on the left, the others are the next three in a half row. The bottom figures are enlarged lateral teeth from various angles (not to scale).



TABLE 1

South African species of *Gulella* with type 'A' radular lateral teeth

| Species                                   | Locality                                          | Formulae             |
|-------------------------------------------|---------------------------------------------------|----------------------|
| <i>Gulella adamsiana</i> (Pfr.)           | Dwesa, nr. Kei River Mouth, Transkei (79-04-15)   | 18-1-18 × 70 to 80   |
| <i>Gulella aliciae</i> (M. & P.)          | St. Lucia Estuary, Zululand (76-08-20)            | 20-1-20 × 80 to 90   |
| <i>Gulella appletoni</i> Van Bruggen      | Sodwana, Zululand Coast (76-03-20)                | 10-1-10 × ?          |
| <i>Gulella aprosdoketa</i> Connolly       | Nr. Hole-in-Wall, Transkei Coast (79-04-15)       | 12-1-12 × 50         |
| <i>Gulella arnoldi</i> (Sturany)          | Coffee Bay, Transkei Coast (77-07-03)             | 10-1-10 × 50         |
| <i>Gulella barnardi</i> Van Bruggen       | Hectorspruit, E. Transvaal (73-04-?)              | 20-1-20 × 120        |
| <i>Gulella barnardi</i> Van Bruggen       | Broham, nr. Nelspruit, E. Tvl. (75-07-26)         | 15-1-15 × 50         |
| <i>Gulella claustralis</i> Connolly       | Coffee Bay, Transkei Coast (77-07-03)             | 9-1-9 × 60           |
| <i>Gulella connollyi</i> M. & P.          | Hennops River, W. of Pretoria, S. Tvl. (76-05-09) | 10-1-10 × 50 to 60   |
| <i>Gulella contraria</i> (Connolly)       | Sabie Caravan Park, E. Tvl. (78-07-23)            | 16-1-16 × 70 to 80   |
| <i>Gulella crassidens</i> (Pfr.)          | Isipingo, nr. Durban, Natal (77-08-20)            | 20-1-20 × 70         |
| <i>Gulella crassilabris</i> (Craven)      | Helsrivier, nr. Witbank, Tvl. (75-11-?)           | 14-1-14 × 70 to 80   |
| <i>Gulella daedalea</i> M. & P.           | Josini Dam, Zululand (75-08-14)                   | 16-1-16 × 80         |
| <i>Gulella daedalea</i> M. & P.           | Umbombo, Lebombo Mts., Zululand (76-05-29)        | 20-1-20 × 90         |
| <i>Gulella delicatula</i> (Pfr.)          | Winterton, Natal (76-09-04)                       | 14-1-14 × 80         |
| <i>Gulella distincta</i> (M. & P.)        | Nr. Montrose, E. Tvl. (73-12-16)                  | 20-1-20 × 140 to 150 |
| <i>Gulella elliptica</i> (M. & P.)        | Jameson's Drift, Zululand (77-04-08)              | 10-0-10 × 60         |
| <i>Gulella gouldi</i> (Pfr.)              | Coffee Bay, Transkei Coast (77-07-03)             | 16-1-16 × 60 to 70   |
| <i>Gulella infans</i> (Craven)            | Hectorspruit, E. Tvl. (73-04-?)                   | 16-1-16 × ?          |
| <i>Gulella infans</i> (Craven)            | Louis Trichardt, N. Tvl. (74-06-?)                | 14-1-14 × 55         |
| <i>Gulella infans</i> (Craven)            | Nr. Krugersdorp, Tvl. (74-07-?)                   | 18-1-18 × 60         |
| <i>Gulella infans</i> (Craven)            | Between Colenso and Weenen, Natal (76-09-05)      | 14-1-14 × 70 to 80   |
| <i>Gulella infrendens</i> (Martens)       | Ballito Bay, N. Coast, Natal (71-04-09)           | 18-1-18 × 80         |
| <i>Gulella infrendens</i> (Martens)       | Westville, Durban, Natal (74-07-?)                | 17-1-17 × 60         |
| <i>Gulella infrendens</i> (Martens)       | Mtubatuba, nr. St. Lucia, Zululand (76-05-29)     | 25-1-25 × 90         |
| <i>Gulella infrendens</i> (Martens)       | Jameson's Drift, Zululand (76-11-21)              | 36-1-36 × 110        |
| <i>Gulella isipingoensis</i> (Stur.)      | Uvongo, S. Coast, Natal (78-11-17)                | 10-1-10 × 50         |
| <i>Gulella kosiensis</i> (M. & P.)        | Nr. Empangeni, Zululand (74-09-?)                 | 20-1-20 × 80         |
| <i>Gulella kraussi</i> (Pfr.)             | Isipingo, nr. Durban, Natal (77-08-20)            | 14-1-14 × 90         |
| <i>Gulella linguidens</i> Connolly        | Josini Dam, Zululand (75-08-14)                   | 12-0-12 × 65 to 70   |
| <i>Gulella maritzburgensis</i> (M. & P.)  | Mhlatuzi River, Eshowe, Natal (76-07-24)          | 20-1-20 × 100        |
| <i>Gulella melvilli</i> (Burnup)          | Jameson's Drift, Zululand (77-04-08)              | 14-1-14 × 50         |
| <i>Gulella perplexa</i> Connolly          | Nkombati, N. Transkei (74-08-?)                   | 14-1-15 × 50         |
| <i>Gulella perspicua</i> (M. & P.)        | Waterval Boven, E. Tvl. (78-07-09)                | 27-1-27 × 90         |
| <i>Gulella perspicuaeformis</i> (Sturany) | Sodwana, Zululand Coast (76-03-20)                | 16-1-16 × 85         |
| <i>Gulella perspicuaeformis</i> (Sturany) | Barberton, E. Tvl. (77-04-10)                     | 16-1-16 × 88         |
| <i>Gulella polita</i> (M. & P.)           | Van Staden's Pass, nr. Port Elizabeth (74-10-15)  | 16-1-16 × 100        |
| <i>Gulella pretoriana</i> Connolly        | Hennops River, W. of Pretoria, S. Tvl. (76-05-09) | 14-1-14 × 80         |
| <i>Gulella puzeyi</i> Connolly            | Port St. John, Transkei (78-03-29)                | 18-1-18 × 125 to 130 |
| <i>Gulella sexdentata</i> (Martens)       | Barberton, E. Tvl. (77-04-10)                     | 20-1-20 × 85 to 95   |
| <i>Gulella umzimvubuensis</i> (Burnup)    | Port St. Johns, Transkei (77-04-30)               | 16-1-16 × 80         |
| <i>Gulella wahlbergi</i> (Krauss)         | Durban, Natal (77-04-21)                          | 18-1-18 × 80         |
| <i>Gulella wendalinae</i> Van Bruggen     | Abel Erasmus Pass, E. v. Tvl. (77-09-05)          | 10-0-10 × 40         |
| <i>Gulella xysila</i> (M. & P.)           | Nr. Krugersdorp, Tvl. (74-07-?)                   | 15-1-15 × 75         |

TABLE 2

South African species of *Gulella* with type 'B' radular lateral teeth

| Species                             | Locality                             | Formulae             |
|-------------------------------------|--------------------------------------|----------------------|
| <i>Gulella triglochis</i> (M. & P.) | Ponta de Oura, Mozambique (73-05-31) | 38-1-38 × 200 +      |
| <i>Gulella triglochis</i> (M. & P.) | Ubombo Township, Zululand (75-08-17) | 45-1-45 × 200 to 250 |
| <i>Gulella queketti</i> (M. & P.)   | Kelso, Natal, S. Coast (78-11-19)    | 38-1-38 × 180        |
| <i>Gulella zuluensis</i> Connolly   | St. Lucia Bay, Zululand (77-07-?)    | 30-1-30 × 220 to 250 |



an angle to the main axis of the tooth. This process protrudes from the base and is embedded in the basal membrane. I have called this process the basal 'anchor' because it could serve to limit the side-to-side movement of the teeth when they are in use. The remainder of the base of the tooth is fairly flat and is in contact with the basal membrane.

The protruding basal 'anchor' varies considerably from species to species, being only vestigial in some, i.e. *G. crassilabris* (Craven), *G. wendalinae* Van Bruggen and *G. barnardi* Van Bruggen, and becomes visible only when stained according to the method outlined above. Although the basal 'anchor' was the main distinguishing feature it was noteworthy that all the species in this group had relatively few teeth in total (i.e. 1000 to 8000), when compared with Type 'B' (13000 to 23000). Type 'A' has from 50 to 150 rows, each row having laterals varying in number from 9 to 36 on each side. The lateral teeth increase in size from number 1 to number 6 or 7 and thereafter diminish in size until the last two or three become rudimentary.

Table 1 lists those species found to have this type of lateral tooth. The identity of the majority has been verified by Dr. A. C. van Bruggen of the Rijksmuseum van Natuurlijke Historie, Leiden, Holland, and the remainder were identified from published descriptions.

#### TYPE 'B' (Fig. 3)

This differs from Type 'A' mainly in respect of the absence of the basal 'anchor'. In addition the area of basal attachment is small in relation to the free cutting point. The total number of teeth is large, the three radulae examined having from 180 to 250 rows consisting of a central tooth flanked by 30 to 45 laterals. The teeth in any one row do not vary very much in size but gradually diminish from the tooth immediately adjoining the central to the outer few which are rudimentary. The laterals are not nearly so robust nor so firmly anchored as in Type 'A'. The species examined are listed in Table 2.

#### TYPE 'C' (Fig. 4)

Only one of the species examined falls into this category. This is *Gulella peakei* Van Bruggen, 1975, found at Sodwana, Zululand Coast, on 76-03-20. The lateral teeth are remarkable for their large area of basal attachment. They are almost as tall as they are long, giving them a very robust appearance. However, they lack the basal 'anchor' of Type 'A'.

This radula has not previously been described and consists of a minute, amorphous central tooth flanked by eight laterals increasing in size from the first to the third, decreasing from the fourth to the sixth, and the seventh and eighth are rudimentary. Thus there are 17 teeth per row and 50 rows, a total of 850; the smallest number observed.

Finally, and perhaps the most remarkable of the radulae examined, is that of *Gulella browni* Van Bruggen 1969, found at Sodwana, Zululand Coast, on 73-03-20. This is another radula not previously described and the teeth are so distinctly different as to warrant special mention. The radula (Fig. 5) has a heart-shaped central tooth flanked by nine laterals. The laterals gradually diminish in size from the first to the sixth, all of which are tricuspid, and thereafter become rudimentary. There are 47 rows of teeth. *Gulella browni* certainly occupies an isolated position among Southern African species as regards its radula.

#### DISCUSSION

In studying these radulae a number of interesting speculations occurred. Why, for instance do so many species possess the basal 'anchor' and sturdy teeth? Is their diet of such a nature that they require the extra support and, what do they eat?



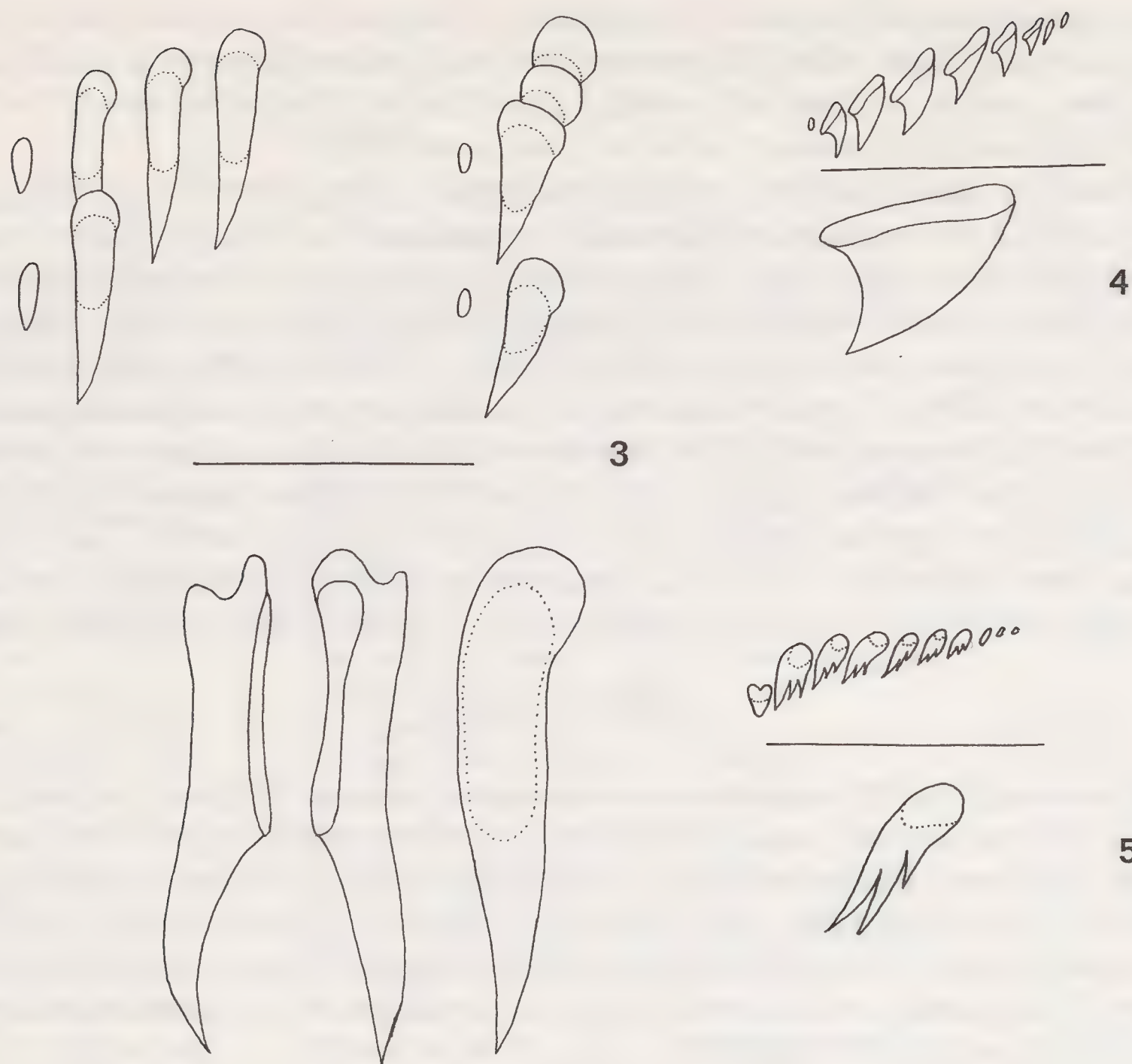


Fig. 3. Radula type 'B' of *Gulella*, upper left *G. triglochis* (M. & P.), upper right *G. natalensis* (Crvn.). Scale 0.05 mm. The central tooth is shown on the left, the others are the adjoining lateral teeth in a half row. The bottom figures are enlarged lateral teeth from various angles (not to scale).

Figs. 4–5. Various radula types of *Gulella*. 4. *G. peakei* Van Bruggen (type 'C'), half row of teeth, note minute amorphous central tooth. Scale 0.05 mm. Bottom figure shows enlarged lateral tooth. 5. *G. browni* Van Bruggen, half row of teeth, note heart-shaped central tooth. Scale 0.05 mm. Bottom figure shows enlarged lateral tooth. Bottom figures not to scale.

Little is known of their microhabitat and diet. Van Bruggen (1967) notes that their food consists of soft invertebrates and that South African streptaxids refused beef in the laboratory. However, Dr. H. E. van Hoepen has established that they will eat liver, somewhat confirming a preference for soft tissues.

There are few confirmatory indications of the basal 'anchor' in the literature available to the author. However, in Connolly's 1939 work there is a drawing of the radula of *Gonaxis vengoensis* Connolly, which indicates a protuberance similar to the basal 'anchor'. In Solem's book (1974) on page 164 there is a SEM photograph showing a dislodged tooth on the radula of *Ptychorhytida aulacospira* (Fig. 10c). This also suggests a protuberance.

Obviously the diet must be quite different for those species with Type 'B' laterals with their weaker basal attachment. These Type 'B' species are all in Connolly's group 2 (1939) and this appears to be the only coincidence of radula with Connolly's groups. All three species are large with simple apertural dentition which little obstructs the aperture. They also have the most numerous teeth per radula.

*Gulella peakei* with Type 'C' laterals is a very small shell, 2 mm in height and 1.5 mm diameter, with a radula 0.5 mm long and 0.5 mm wide. One wonders what its diet must be, especially in view of the robustness of the individual teeth.



*Gulella browni* is also a fairly small shell, 3 mm in height and 1·7 mm major diameter, with a radula measuring 0·3 mm in length and 0·4 mm wide. Here we have the puzzling tricuspid laterals which are not rigid, as in Types 'A', 'B' and 'C', but flexible. They distorted when the cover slip was placed on the slide and resumed their shape on releasing the pressure. These teeth are obviously designed for an entirely different diet from those with rigid laterals. No similar radula can be found in the literature available to the author.

#### ACKNOWLEDGEMENTS

I am indebted to Dr. H. E. van Hoepen for his advice, support and encouragement in preparing this article and for making available the valuable material to me. My thanks are also due to Dr. A. C. van Bruggen who meticulously identified many of the doubtful species that came to hand and prepared the manuscript for the press.

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# THE IDENTITY OF *HELIX SEMINIUM* MORELET (PULMONATA: ENDODONTIDAE)

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(Read before the Society, 18 October 1979)

*Abstract:* An examination of the types of *Helix seminium* Morelet in connection with the naming of a collection sent to me from Liverpool Museum by Mrs. N. F. McMillan has shown them to be conspecific with *Afropunctum zanguebaricum* (Craven). Morelet's name supplies the earliest epithet for this species which must now be called *Afropunctum seminium* (Morelet). A revised map of the geographical distribution is given and brief notes on the radula. Its placing in the Endodontidae is confirmed.

Amongst the final lot of African material from the Salisbury collection sent to me by Mrs. N. F. McMillan from the Liverpool Museum for naming was a box of three small shells bearing the following data: *seminium* Morelet, Bunso Plantation, Bosuso, Gold Coast, G.C. Spence. I had never previously had any need to investigate this species and was startled to discover that the specimens were undoubtedly the species I had optimistically hoped was finally to be called *Afropunctum zanguebaricum* (Craven). Fortunately I have a copy of Morelet's paper (1873) and the description is as follows: 'T[esta] parvula, imperforata, obtuse turbinata, tenuis, rufocornea, parum nitens, omnino glabra; anfr.  $4\frac{1}{2}$ -5 convexiusculi, ultimus leviter depressus, subtus convexior et nitidior; apert. obliqua, depressa lunaris, marginibus simplicibus, rectis, columellari superne vix reflexiusculo. - Diam. maj.  $3\frac{1}{3}$ , min. 3, altit. 3 mm. Habitat in prov. Gabon. Helici fulvae persimilis; differt spira magis depressa et anfractuum numero minore ab H. parvula Rang statura anfractuum numero et perforationis defectu distinguitur.' As far as it goes this fits the species concerned save for the 'imperforata' but unfortunately the details of sculpture are not mentioned although the mention of a difference in gloss between the upper and lower surfaces suggests that that too is correct. Fortunately the types of Morelet's species are preserved at the British Museum (Nat. Hist.). (Reg. nos. 1893.2.4.990-2) and I have been able to directly compare them with the types of *Helix zanguebarica* Craven also preserved at the British Museum (Reg. nos. 1891.3.7.16-18). There is absolutely no doubt that they are conspecific. Both are narrowly perforate. This unfortunately means another name change for the species and I hope the final one. Synonymy is detailed below.

## ***Afropunctum seminium* (Morelet 1873)**

- 1873 *Helix seminium* Morelet: 329
- 1880 *Helix zanguebarica* Craven: 217, pl. 22 fig. 4a, b, c
- 1912 *Thapsiella connollyi* Preston: 70, fig. 3
- 1919 ?*Sitala kigomaensis* Germain: 351, figs. 32, 33
- 1934 *Afropunctum mermodi* Haas: 221, fig. 1
- 1939 *Kaliella connollyi* (Preston); Connolly: 165
- 1959 *Afropunctum mermodi* Haas; Verdcourt: 91
- 1961 *Thapsia vesti* sensu Sparks & Grove: 359, pl. 2, figs. K-M, non Jickeli
- 1963 *Afropunctum zanguebaricum* (Craven); Verdcourt: 158, map.
- 1966 *Afropunctum zanguebaricum* (Craven); van Bruggen: 343



The map I gave in 1963 was inadequate at the time of publication since I inadvertently omitted the type locality of *A. mermodi* given by Haas as Katanga, Luluabourg but that town is not in Shaba (= Katanga) but in Kasai. A new map is given here from which it can be seen that the species is very widely distributed in Tropical Africa and doubtless much overlooked due to its small size. Its distribution can now be summarized as follows.

## DISTRIBUTION

SAHARA: Tibesti: Begour Crater (Quaternary), A. T. Grove.

GHANA: Bosuso, Bunso Plantation, G. C. Spence.

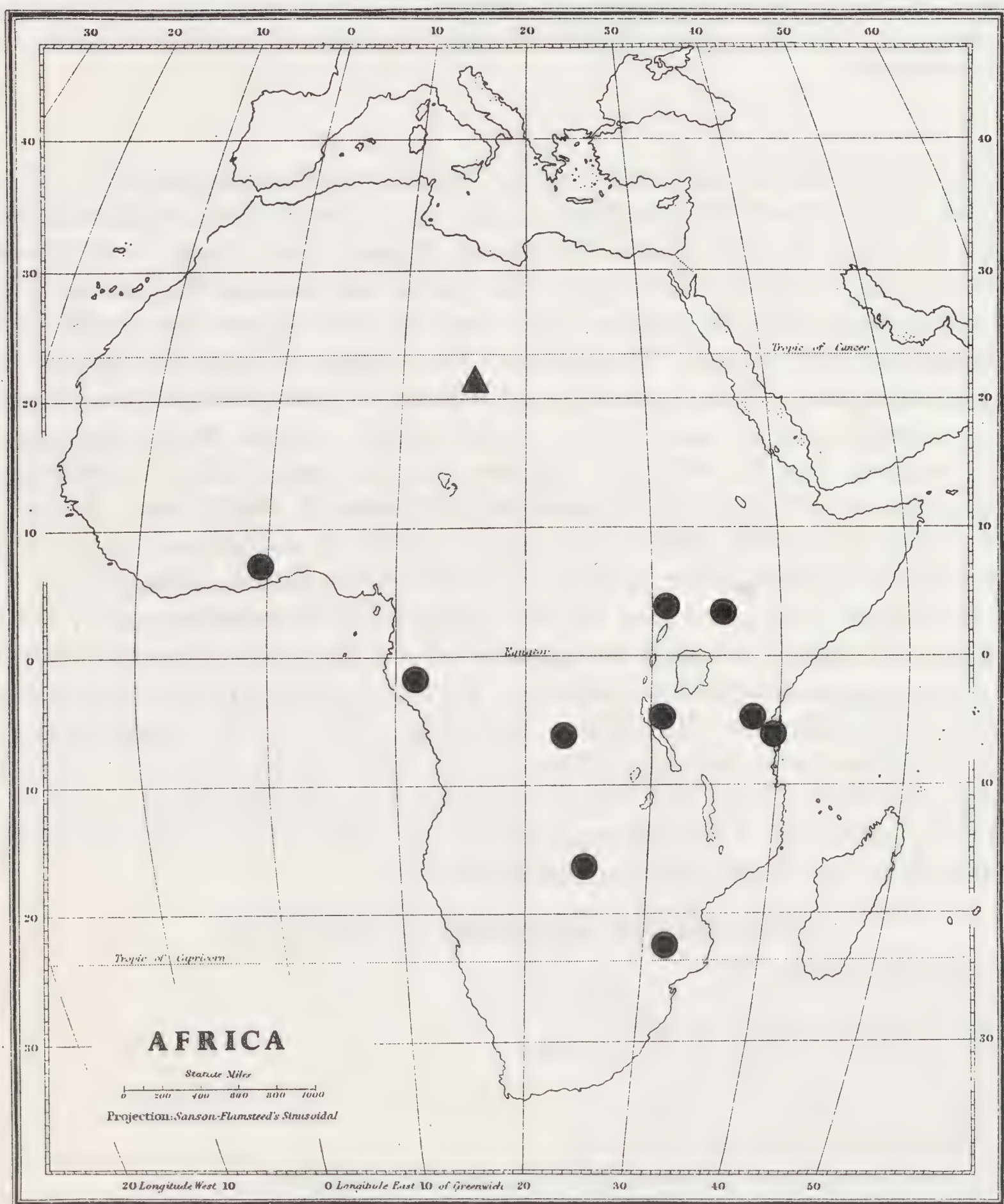
GABON: Without exact locality, Cl. Marche & de Compiègne.

ZAIRE: Kasai: Luluabourg, ?Romieux.

UGANDA: West Nile: Rhino Camp, W. Wilkinson.

KENYA: Turkana: Turkwell River Drift, C. F. Hemming.

TANZANIA: East Usambara foothills: Magila, A. E. Craven; Western Province: Kigoma, collector?; Zanzibar, J. Gibbons.



Distribution of *Afropunctum seminum* (Morelet). Recent (dots); Quaternary (triangle).



RHODESIA: Victoria Falls, M. Connolly.

SOUTH AFRICA: Transvaal: Kruger National Park, van Bruggen *et al.*

In my 1963 note I also made a second careless error. I stated that 'unfortunately no living examples have yet been preserved' but the type material of *A. mermodi* was collected in spirit but later dried out and is too contorted for dissection. I did, however, prepare a radula from material kindly sent by Dr. E. Binder from Geneva with permission to destroy a shell. Unfortunately I was not certain at the time even after examining the radula to which group the genus belonged. Some 15 years later I found my notes on this radula. The formula is probably 15, 2, 4, c, 4, 2, 15, there being 4 true laterals and 2 transitionals; the outermost teeth have details beyond the resolution of the microscope I was using. Some selected teeth are illustrated in Fig. 1. Dr. A. Solem has examined this figure and thinks the radula indicates a genus near to *Punctum* thus confirming the usual placing in Endodontidae although in my list of genera (1972) I had placed it near to *Guppya* and *Kaliella* in the Euconulidae. Well-preserved material is required so that the genital anatomy can be worked out. I am, however, now convinced that the species is to be placed near *Punctum* and have followed this placing in my Check-list of East African non-marine Mollusca (in preparation).

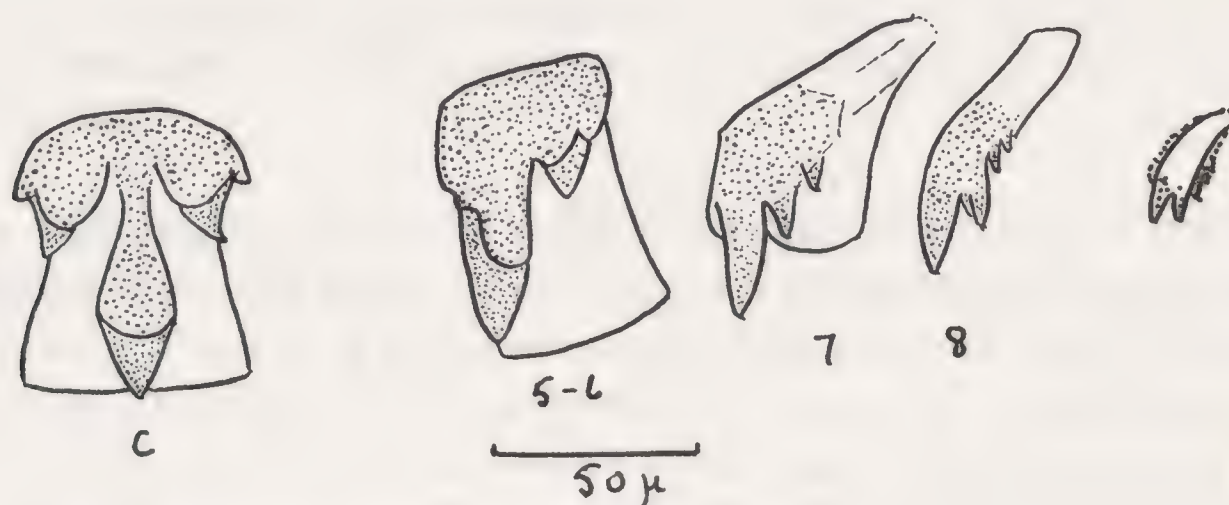


Fig. 1. *Afropunctum seminium* (Morelet). Selected teeth from radula.

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# *PARMACELLA* (PULMONATA: PARMACELLIDAE), A SLUG NEW TO THE PLEISTOCENE OF BRITAIN

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(Read before the Society, 13 December, 1980)

*Abstract:* *Parmacella*, a genus of slugs having at the present day a mainly mediterranean distribution, is recorded as a fossil for the first time in northern Europe, from Lower Pleistocene deposits at Bramerton, Norfolk.

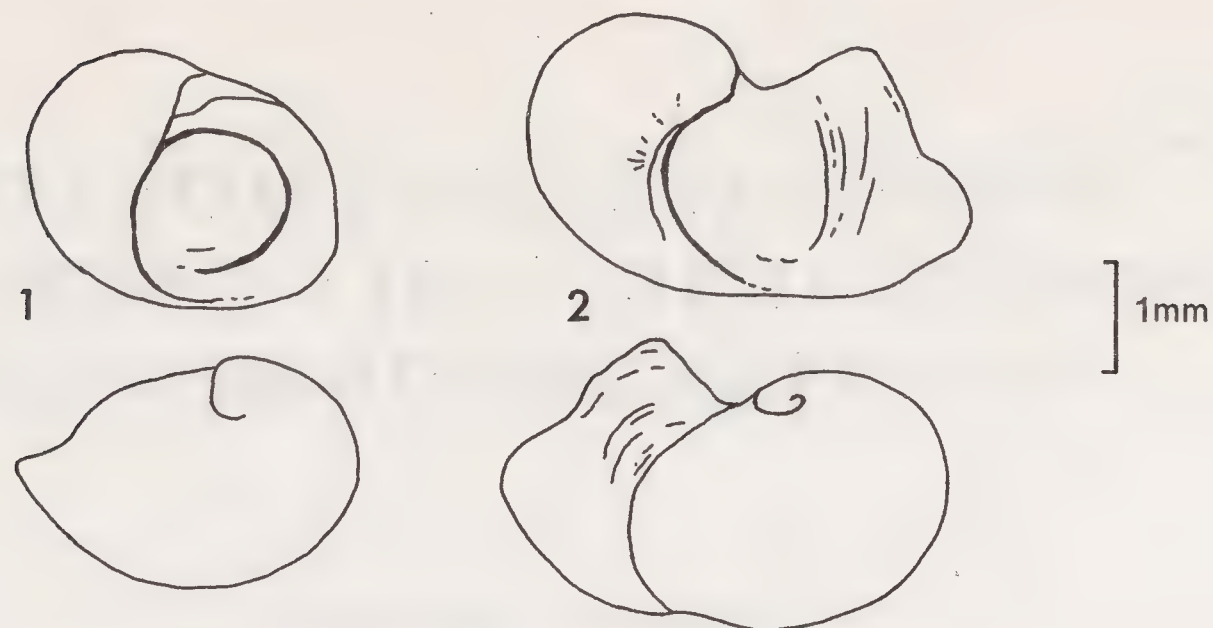
In 1974 a section was re-dug by the Geological Society of Norfolk in Blake's Pit, Bramerton, Norfolk (TG 298061) and the lower part of the local Norwich Crag series (Icenian: Lower Pleistocene) was exposed. In the early literature this was referred to as the Mammaliferous Crag or the Fluvio-marine Crag due to the presence of numerous mammalian remains and non-marine shells. The shelly marine sands seen near the base of the section in 1974 were found to contain a relatively high proportion of land and freshwater shells. Among these were a number of small shells, of approximately  $1\frac{1}{4}$  whorls, resembling a juvenile *Theodoxus* in general shape (Fig. 1). A few examples showed the development of a thin, convex, plate-like adult shell (Fig. 2). It was decided that these could only be the shells of a slug of the family Parmacellidae.

The shells were compared with a specimen of *Parmacella valencienii* Webb & van Beneden (= *P. moquini* Bourguignat; Germain, 1930, p. 112) from Gibraltar and no significant differences could be detected. A shell of this species from Gibraltar is figured by Kerney (1980, p. 234). However, the Bramerton specimens were incomplete, with the thinner part of the shell broken, and it is not certain that species of *Parmacella* can be determined from the shell alone. *P. valencienii* is found living in southern France, Spain, Portugal and north Africa. The family occurs from the Canary Islands to the Middle East (Zilch, 1959, p. 264). *Parmacella* is recorded fossil from early Pleistocene deposits in Hungary (Krolopp, 1973) but has not previously been recognized from the Pleistocene of northern Europe. Specimens from Bramerton have been deposited in the British Museum (Natural History), the Sedgwick Museum, Cambridge, and the Castle Museum, Norwich.

The finding of a southern terrestrial species like this in the Norwich Crag raises interesting questions as to the climate of the period. The Icenian marine deposits of East Anglia are known to span a series of glacial and interglacial episodes (West, 1961). Recently, the lower deposits at Blake's Pit, Bramerton, have been shown to belong to an *Alnus-Quercus-Carpinus* pollen biozone within a temperate stage, for which the new name Bramertonian is proposed (Funnell *et al.*, 1979, p. 497).

I should like to thank Dr. M. Kerney for originally suggesting the genus *Parmacella* from a sketch, Dr. R. C. Preece for drawing the figures, Mr. A. Norris for the loan of a specimen of *P. valencienii*, Mr. T. Meijer for checking fossil records from Holland, and Mr. A. Janssen for helpful suggestions.





Figs. 1 and 2. *Parmacella* sp., Blake's Pit, Bramerton. BMNH (Dept. of Palaeontology) reg. nos. GG 9143-4.

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# THE VALUE OF SHELL MICROSCULPTURE AS A GUIDE TO THE IDENTIFICATION OF LAND MOLLUSCA FROM QUATERNARY DEPOSITS

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(Read before the Society, 13 December, 1980)

*Abstract:* Land Mollusca are common fossils in Quaternary sediments and their analysis for environmental study is now standard practice. Literature for identifying fossil shells is scanty and generally relies on characters present only in adults. Since most fossil samples are composed largely of fragmentary or juvenile shells other characters must be used. Differences in shell microsculpture are often diagnostic. A selection of scanning electron photomicrographs illustrating many of the commoner species present in British Postglacial deposits is presented in order to facilitate specific determination of fossil material.

## INTRODUCTION

The analysis of the land snails present in many Quaternary deposits can yield much information on environmental and climatic history. In addition the technique has been used to detect the influence of early man on the landscape as well as a means of relative dating. The technique is particularly valuable since it can be applied to calcareous sediments where oxidation generally precludes pollen analysis.

Correct interpretations clearly depend on the accuracy with which the species of the fossil mollusc assemblage can be identified. Many problems are encountered when attempting to name fossil material. First, the brightly coloured patterns characteristic of several species of snail are often not preserved. Secondly the shells of several species are covered with periostracal hairs (e.g. *Trichia hispida*, *Ashfordia granulata*) or even spines (*Acanthinula aculeata*). These structures are seldom preserved in fossils, though the shell surface may be covered with hair pits marking points of attachment.

In spite of these difficulties, the identification of adult specimens is relatively straightforward, given a little experience, and reference can be made to standard texts. However, since the majority of fossils recovered are juveniles or small fragments of larger shells, the problems of identification increase proportionately; for early workers a point was reached where the specimen became too small to be named with confidence and these shells were listed as indeterminate. The characters used for naming immature shells are often rather different from those used when naming adults. Indeed certain species that are quite distinct when adult are remarkably similar at the 1-2 whorl stage. There are very few accounts that deal specifically with such juvenile or fragmentary material. A notable exception is the book by Ložek (1964) on the Quaternary Mollusca of Czechoslovakia, and that by Evans (1972), which includes a series of outline drawings illustrating the growth stages and characteristic fragments of most of the British land Mollusca. Three other papers are noteworthy. Kennard *et al.* (1925) examined the problems encountered when naming fossil Unionacea from the British Quaternary and illustrate some diagnostic characters present in immature shells. Two other papers (Kerney, 1963; Kerney *et al.*, 1964) describe the molluscan faunas from Late-glacial and Postglacial



deposits from the chalklands of southern Britain and are concerned primarily with the identification and analysis of land Mollusca.

Although features such as the tightness of coiling or depth of suture are very important it has been found that variations in shell microsculpture are among the most useful characters for identification in fossils. Paradoxically it is often easier to separate certain species when fossil than when alive; for example, juveniles of species of *Aegopinella* and *Oxychilus* are often more readily distinguished when fossil than in the living state, when the periostracum conceals all-important shell details.

In quantitative environmental studies it is necessary to identify and count every shell apex, thereby avoiding the danger of counting the same specimen twice. Occasionally non-apical fragments of larger species unrepresented by apices also require identification. It is therefore essential to name as many specimens as possible and to reduce the number listed as indeterminate to a minimum. This is particularly important when low numbers of shells are recovered from poor samples. In practice it has been found that nearly all specimens are identifiable provided that the preservation is good.

The object of the following notes is to facilitate specific determination of fossil material when broken or juvenile. The study arose directly from my research on the Mollusca of certain early Postglacial deposits (mainly calcareous tufas) in southern Britain (Preece, 1978) and is concerned primarily with the difficulties which I encountered in naming fossil shells from these deposits. Many of the species illustrated are also common in Quaternary deposits of other ages and types, though it should be borne in mind that the occurrence elsewhere of perhaps rather different assemblages of species may offer problems not covered here. A scanning electron microscope (SEM), offering high resolution and very great depth of focus, has been used to illustrate variations in shell microsculpture as well as the more subtle differences in whorl form. This technique is playing an increasingly important role in molluscan taxonomy (e.g. Solem, 1976; Gittenberger, 1977). It should be emphasized that all the structures illustrated can be detected using a good light microscope; the SEM has only been used for illustrative purposes. No photographs however can replace a good set of reference material.

#### SOURCE OF MATERIAL ILLUSTRATED

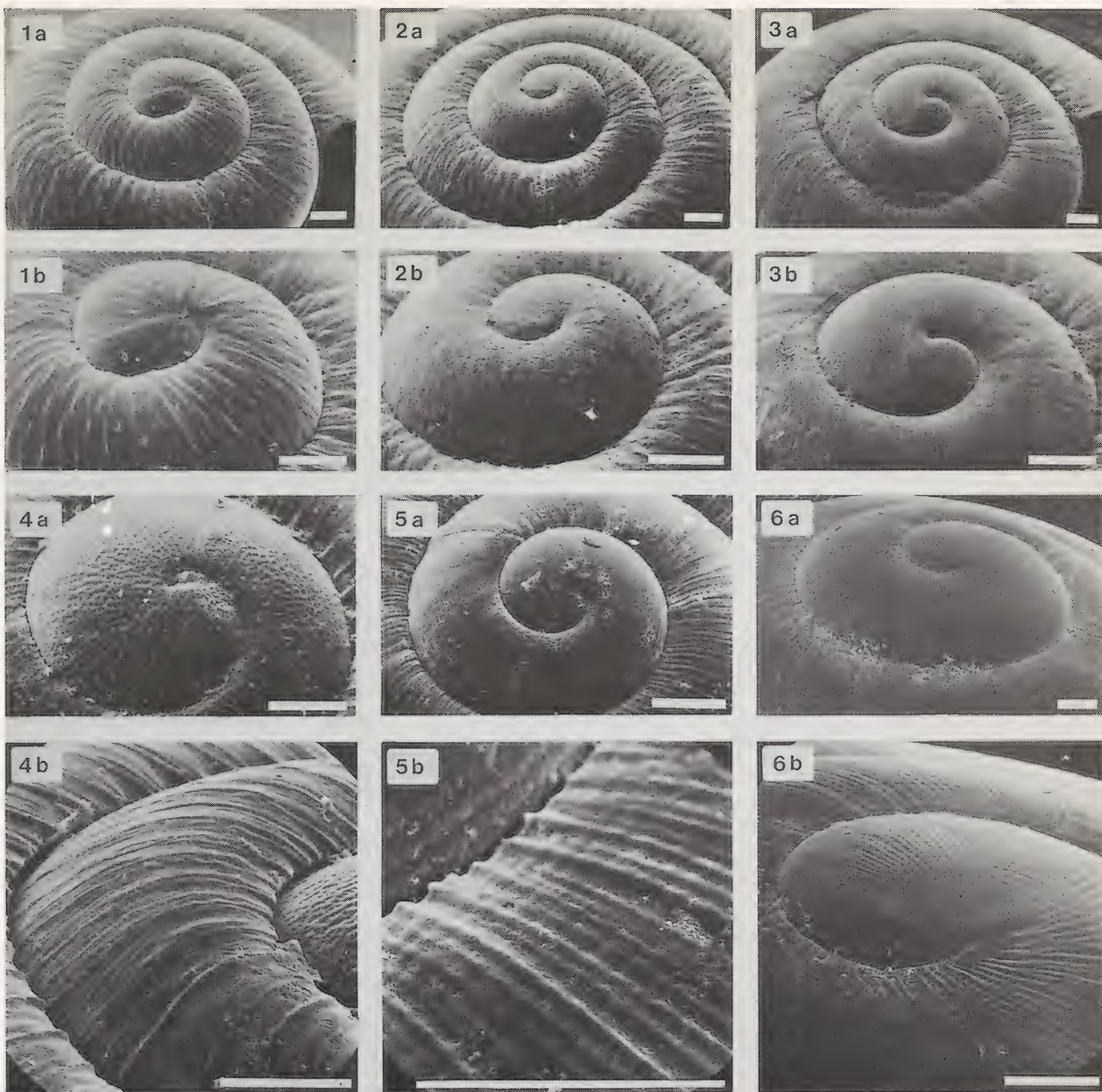
The source of the specimens illustrated is given below.

- (1) Watlingbury, Kent (TQ 687534). Sample from the upper third of the tufa (Kerney *et al.*, 1980).
- (2) Blashenwell, Dorset (SY 952805). Sample from the upper part of the tufa (Preece, 1980).
- (3) Caerwys, Flintshire (SJ 128138). Sample from the middle part of the tufa (Preece, 1978).
- (4) Eastham Grange, Worcestershire (SO 671676). Sample from near base of early Postglacial tufa (R. C. Preece, unpublished).
- (5) Kingstone Winslow, Berkshire (SU 263856). Postglacial deposit exposed in stream section (R. C. Preece, unpublished).
- (6) Tornewton Cave, Devon (SX 817673). Postglacial cave earth (Kerney, 1976).
- (7) Cow Gap, Eastbourne, Sussex (TV 595957). Late-glacial slope deposit (Kerney, 1963).
- (8) Rodney Stoke, Somerset (ST 481498). Basal third of tufa (M. J. Willing, unpublished).

#### SUITABILITY AND PREPARATION OF SPECIMENS

The sediments listed above are predominantly tufas, deposited by hard-water springs and streams. The preservation of the contained Mollusca is consequently excellent and even the finest details of shell microsculpture are usually preserved. Such material is ideal for study under the SEM. The preservation of the surface detail of shells in other deposits is often inferior and surfaces may be pitted or corroded. Nevertheless, provided that leaching and other corrosive processes have not been too severe, it is even here possible to recognize specific differences between closely related species.





### PLATE 13

Figs. 1–3, Scale bars represent 200  $\mu\text{m}$ ; Figs. 4–6, Scale bars represent 100  $\mu\text{m}$ .

Fig. 1 a, b. *Ashfordia granulata* (Alder). Blashenwell.

Fig. 2 a, b. *Trichia hispida* (L.). Wateringbury.

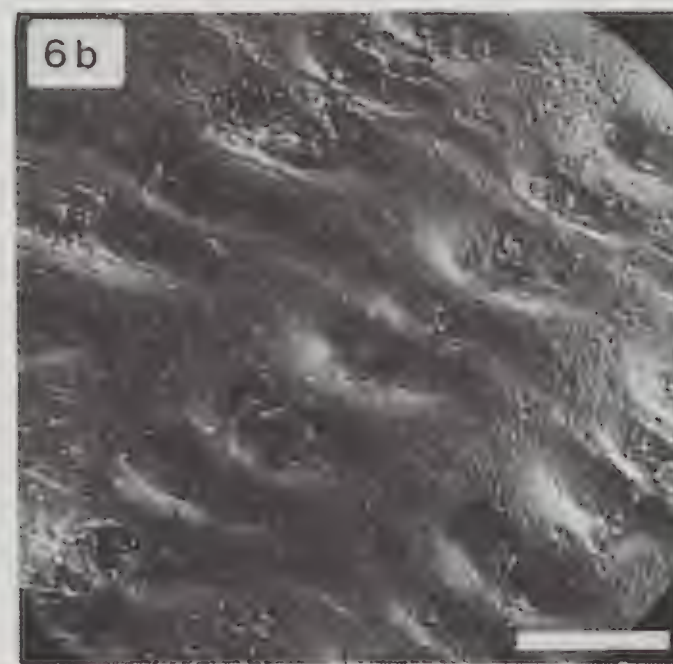
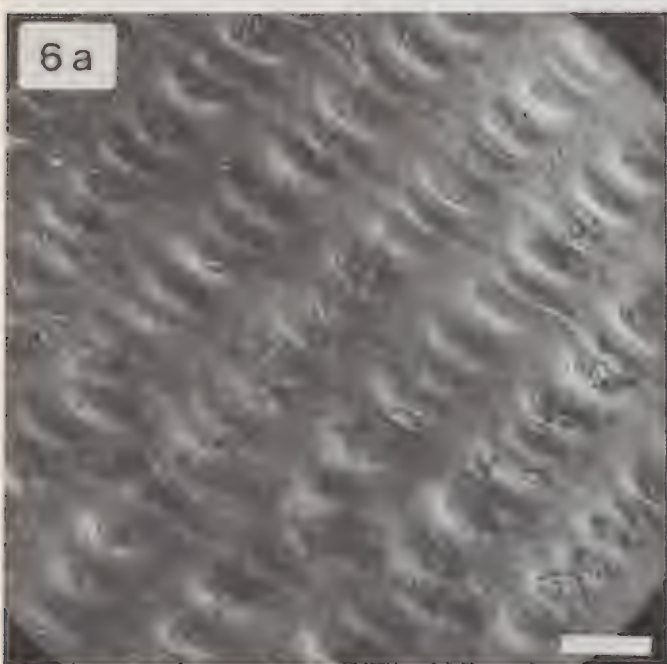
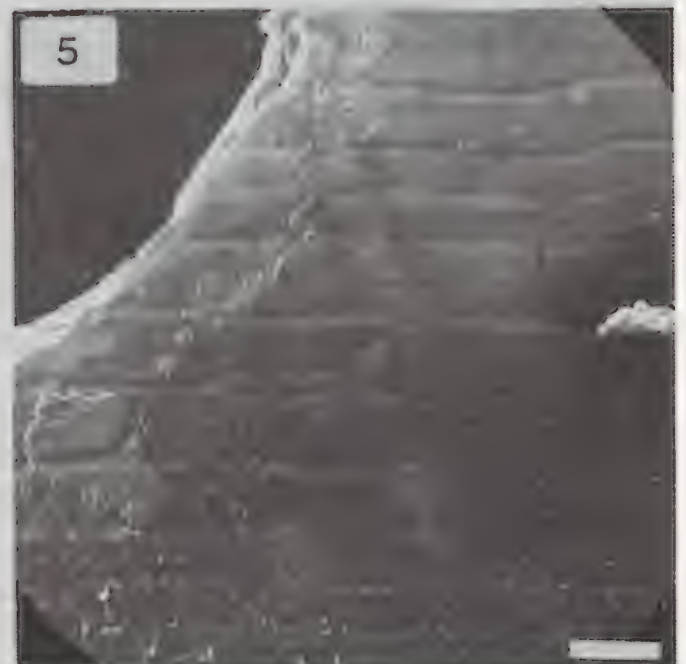
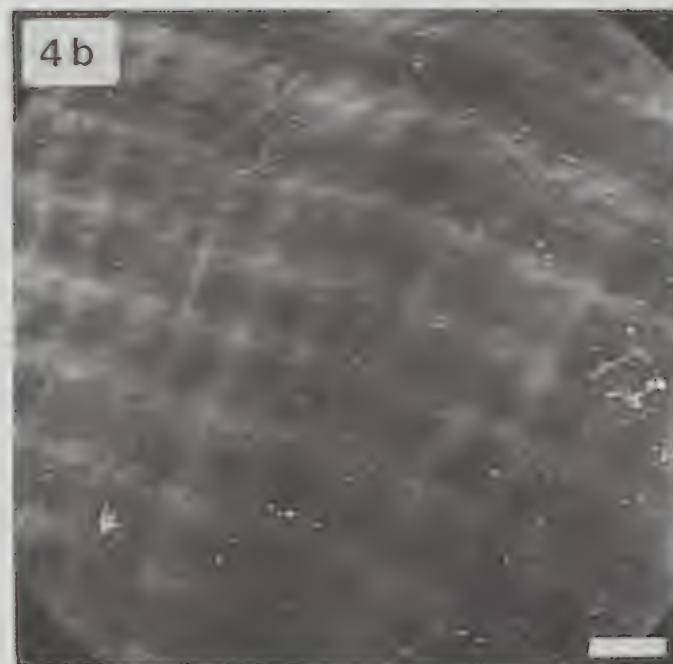
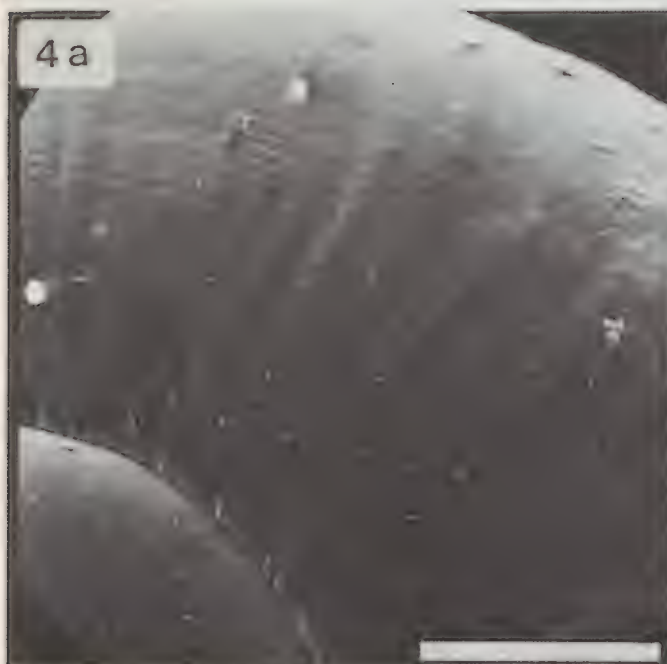
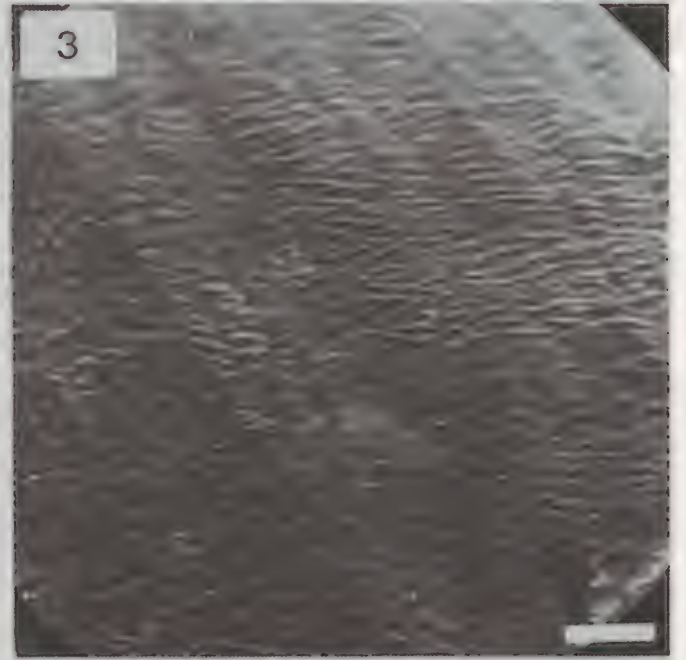
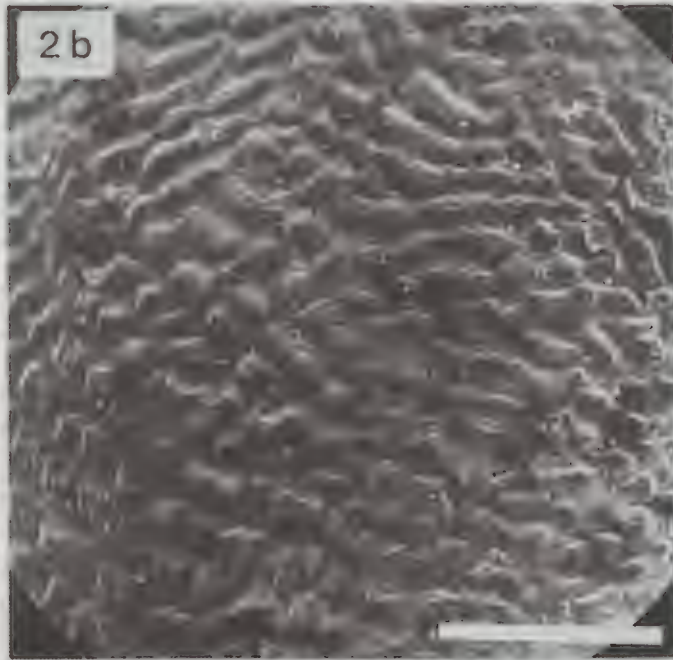
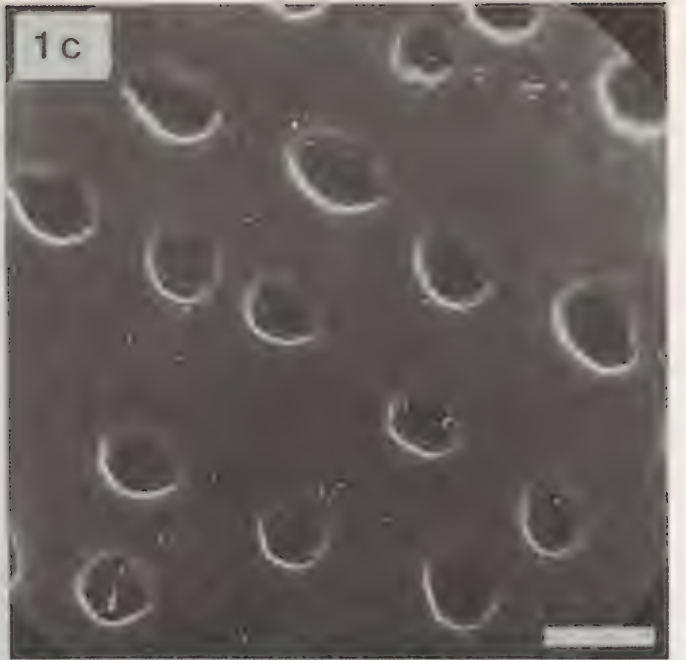
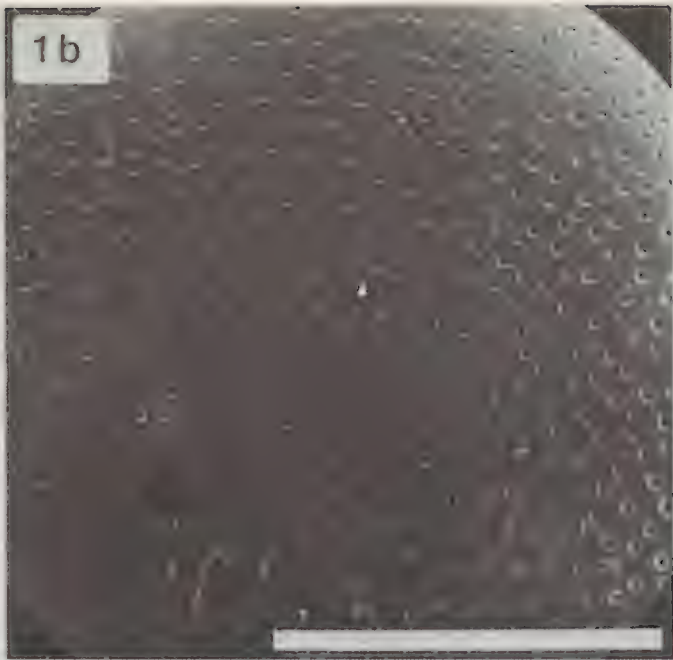
Fig. 3 a, b. *Trichia striolata* (Pfeiffer). Wateringbury.

Fig. 4 a, b. *Spermodea lamellata* (Jeffreys). Wateringbury.

Fig. 5 a, b. *Punctum pygmaeum* (Draparnaud). Wateringbury. (a) apical view (b) detail of suture of second whorl.

Fig. 6 a, b. *Euconulus fulvus* (Müller). Wateringbury.







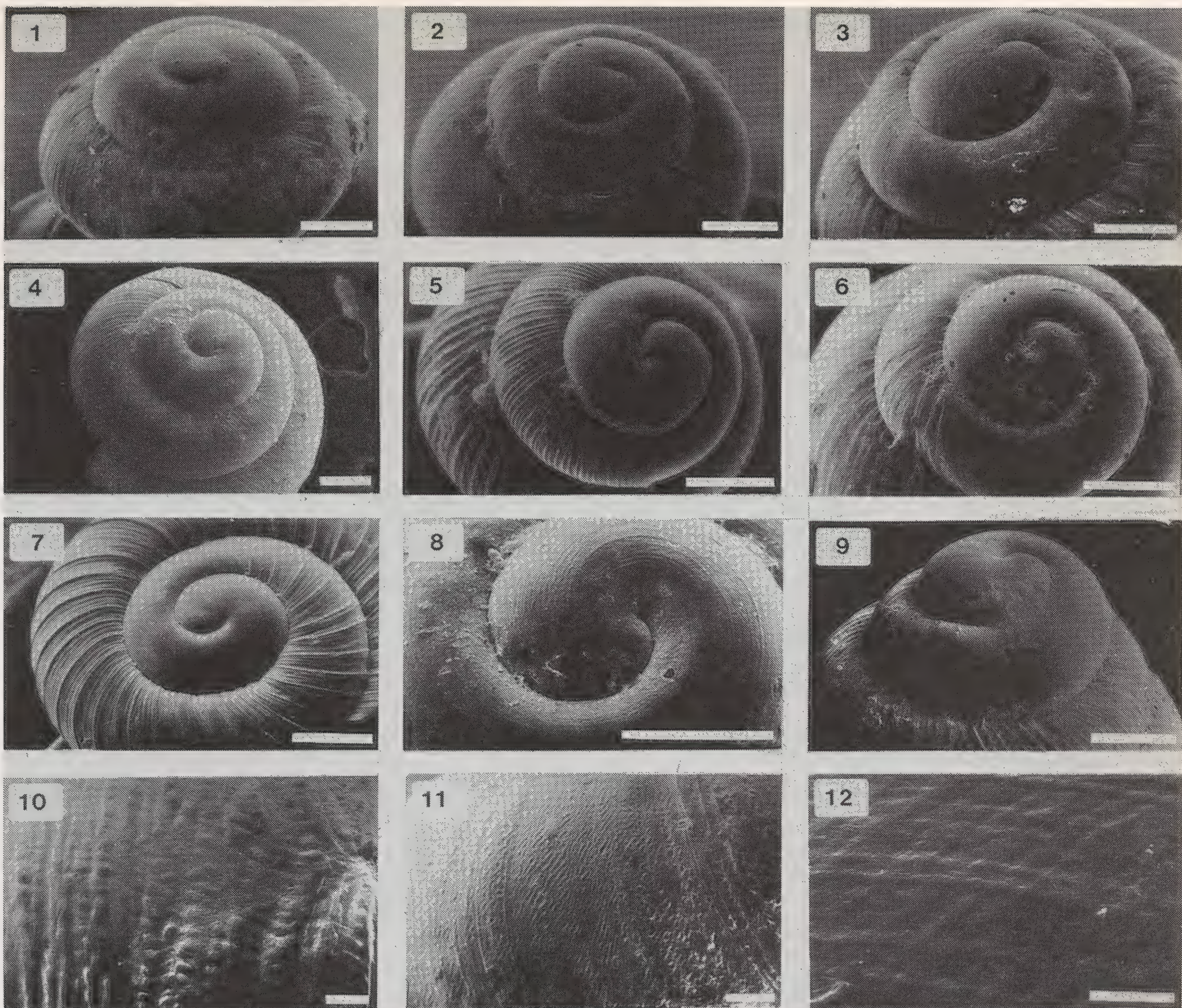


PLATE 15 (above)

Scale bars represent 200  $\mu\text{m}$  except Fig. 12 where it represents 40  $\mu\text{m}$ .

- Fig. 1. *Lauria cylindracea* (da Costa). Watringbury.
- Fig. 2. *Leiostyla anglica* (Wood). Watringbury.
- Fig. 3. *Pupilla muscorum* (L.). Caerwys.
- Fig. 4. *Vertigo moulinsiana* (Dupuy). Watringbury.
- Fig. 5. *Vertigo substriata* (Jeffreys). Watringbury.
- Fig. 6. *Columella edentula* (Draparnaud). Watringbury.
- Fig. 7. *Vallonia costata* (Müller). Blashenwell.
- Fig. 8. *Acanthinula aculeata* (Müller). Watringbury.
- Fig. 9. *Abida secale* (Draparnaud). Cow Gap.
- Fig. 10. *Ena montana* (Draparnaud). Kingstone Winslow.
- Fig. 11. *Ena obscura* (Müller). Watringbury.
- Fig. 12. *Zenobiella subrufescens* (Miller). Tornewton Cave. Fragment of body whorl.

PLATE 14 (opposite)

Scale bars represent 200  $\mu\text{m}$ , except Figs. 1c, 4b & 7 where they represent 10  $\mu\text{m}$ .

- Fig. 1 a-c. *Vitrina pellucida* (Müller). Eastham. Juvenile shell.
- Fig. 2 a, b. *Helicigona lapicida* (L.). Watringbury. Apical fragment.
- Fig. 3. *Cepaea nemoralis* (L.). Blashenwell. Microsculpture of body whorl.
- Fig. 4 a, b. *Aegopinella pura* (Alder). Watringbury. Microsculpture of juvenile shell.
- Fig. 5. *Arianta arbustorum* (L.). Blashenwell. Fragment of body whorl.
- Fig. 6 a, b. *Pomatias elegans* (Müller). Watringbury. Fragment of body whorl.
- Fig. 7. *Pupilla muscorum* (L.). Caerwys. Microsculpture of apex.





# PLATE 16

Scale bars represent 400  $\mu\text{m}$  except Fig. 2 where it represents 200  $\mu\text{m}$ .

- Fig. 1a, b. *Acicula fusca* (Montagu). Watringbury.
- Fig. 2. *Nesovitrea hammonis* (Ström). Watringbury.
- Fig. 3. a, b. *Oxychilus cellarius* (Müller). Watringbury.
- Fig. 4 a, b *Aegopinella nitidula* (Draparnaud). Watringbury.
- Fig. 5. *Discus rüderatus* (Férussac). Rodney Stoke.
- Fig. 6 a,b. *Discus rotundatus* (Müller). Watringbury.
- Fig. 7. *Balea perversa* (L.). Watringbury.
- Fig. 8. *Clausilia bidentata* (Ström). Watringbury.
- Fig. 9. *Cochlodina laminata* (Montagu). Watringbury.



Each specimen selected for illustration was carefully examined under a binocular light microscope for traces of adhering sediment. These were removed with de-ionised water applied with a fine paint-brush. The specimens were then mounted on stubs with double-sided adhesive tape. A conductive paint was applied to areas of poor contact between shell and tape to ensure good electrical conductivity, preventing the build-up of an electrical charge on the specimen when being scanned. The stubs were then placed for about 3 minutes in a polaron E 5000 diode sputter coater depositing a uniform film of gold about 35–40 nm thick.

All the photomicrographs were taken in the Department of Geology, Imperial College, London using either a Cambridge S 600 or JEOL JSM-35. The specimens have been deposited in the Department of Palaeontology, British Museum (Natural History).

#### IDENTIFICATION NOTES

The nomenclature used follows Kerney and Cameron (1979).

*Pomatias elegans*. Plate 14, Fig. 6a, b.

The shell is thick and carries a series of transverse and spiral ribs readily observable in small fragments. The inner surface is polished and is frequently bright yellow or orange and consequently conspicuous amongst shell debris. Because of the thickness of the shell, this species is prone to derivation and careful note should be made of condition (*i.e.* whether fresh or worn).

*Acicula fusca*. Plate 16, Fig. 1a, b.

Small juveniles are unlikely to be confused with any other species, except perhaps *Carychium*. *A. fusca* has a blunter apex, shallower suture and a glossy shell with sharply incised vertical grooves that are readily detectable in small fragments.

*Columella* spp. Plate 15, Fig. 6.

Juveniles can be distinguished from *Vertigo* by their larger size, coarser growth lines and more loosely coiled protoconch. The differences between *C. edentula*, *C. aspera* and *C. columella* have recently been discussed by Paul (1975) who also gives a series of stereoscan pictures.

*Vertigo* spp. Plate 15, Figs. 4 & 5.

With the exceptions of *V. substriata*, which has a ribbed shell, and of the two sinistral species (*V. pusilla*, *V. angustior*) apices of *Vertigo* are very hard to name. The species present in any sample and their relative proportions can only be gauged from an examination of the diagnostic apertural fragments. *V. moulinsiana* is the largest British species possessing the biggest protoconch (Plate 15, Fig. 4) but this is still considerably more tightly coiled than in *Leiostyla* or *Lauria*. Further details of the separation of *Vertigo* apices are given by Evans (1972, pp. 58–59).

*Abida secale*. Plate 15, Fig. 9.

The apex is similar to that of *Pupilla* but is generally more pointed and markedly conical in outline. Moreover the shell surface is often more coarsely striated.

*Pupilla muscorum*. Plate 15, Fig. 3; Plate 14, Fig. 7.

Juvenile shells lack teeth, a character that separates them from *Lauria* or *Leiostyla*. In addition, the protoconch is rather larger and more bulbous and the umbilicus more open. The whorl profile is more rounded and the suture deeper. The surface is matt and under very high magnification an intricate polygonal network can be seen (Plate 14, Fig. 7).

*Lauria cylindracea*. Plate 15, Fig 1; *Leiostyla anglica*. Plate 15, Fig. 2.

The apical characters of these species are distinctive. *L. cylindracea* has a flattened apex



which sometimes appears to have a radially flecked surface. The suture is very shallow. The apex of *L. anglica* is smaller with a somewhat deeper suture. The parietal and columellar folds appear early in both species which are therefore readily separable from the equivalent stages of *Pupilla* and the larger Vertiginidae.

Shell colour, if preserved, can be used as an additional guide. Shells of *L. anglica* are often a rich chestnut with a pale basal area while those of *L. cylindracea* tend to be uniformly buff. However this is not a reliable criterion since pale forms of *L. anglica* sometimes occur.

*Vallonia* spp. Plate 15, Fig. 7.

The distinguishing features of adult *Vallonia* are described by Sparks (1953). In addition to the strong transverse ribbing, faint spiral lines can also be seen around the apex of *V. costata* (cf Gittenberger, 1977). The whorls are also more shouldered than in the other two common British species (*V. pulchella*, *V. excentrica*), a feature which can be used to name even weathered, almost ribless, shells.

*Acanthinula aculeata*. Plate 15, Fig. 8.

The protoconch differs from that of *Spermodea* in being slightly larger and its characteristic sunken form distinguishes it from any pupillid. Its surface carries a series of irregular spiral raised lines, enabling non-apical fragments to be recognized. The periostracal spines are not preserved in fossils; SEM photographs illustrating a modern shell are given by Gittenberger (1977).

*Spermodea lamellata*. Plate 13, Fig. 4a, b.

The complex transverse ribbing, and tightness of coiling, coupled with the shouldered whorl profile and squat appearance, are characteristic. The rough texture of the protoconch gives rise to a pearly lustre when viewed under binocular microscope. The ribbing begins at about the  $1\frac{1}{2}$ –2 whorl stage.

*Ena montana*. Plate 15, Fig. 10; *Ena obscura*. Plate 15, Fig. 11.

The bulbous, obtuse apices of *Ena* are distinctive. Only *E. obscura* occurs at all frequently as a fossil, and a careful search should be made for non-apical fragments. The microsculpture of *E. obscura* is largely composed of a series of oblique flutings; that of *E. montana* is much coarser with distinct spiral striations cutting across the irregular growth ridges and giving a file-like appearance.

*Punctum pygmaeum*. Plate 13, Fig. 5a, b.

The protoconch is very tightly coiled and its surface has a silky appearance due to a fine spiral microsculpture.

*Discus ruderatus*. Plate 16, Fig. 5; *Discus rotundatus*. Plate 16, Fig. 6a, b.

Juveniles and apical fragments of *D. ruderatus* can be distinguished from those of *D. rotundatus* by their more rapidly expanding whorls, more widely and regularly spaced ribs and their blunter periphery. The striped colour pattern characteristic of *D. rotundatus* is never seen in *D. ruderatus* but the delicate transverse ribbing begins at a slightly earlier stage, becoming gradually coarser. In *D. rotundatus* the ribbing does not appear under about the 2 whorl stage. Very young shells somewhat resemble *Aegopinella pura* but they lack the spiral sculpture, have a slightly deeper suture and a wider but shallower umbilicus.

*Vitrina pellucida*. Plate 14, Fig. 1a–c.

In fossils, the translucence of the shell approaches that of the Zonitidae but *Vitrina* can be distinguished by its rapidly expanding whorls and series of nearly circular pits arranged spirally



around the apex. Although *V. pellucida* is by far the commonest fossil species in Britain it should be noted that this pitting also characterises other palaeartic Vitrinidae (e.g. *Phenacolimax* and *Semilimax*). Further work may enable taxonomic separation.

*Nesovitrea hammonis*. Plate 16, Fig. 2; *Nesovitrea petronella*.

The upper surface of *Nesovitrea* is characterized by strong radial furrows. The suture is shallower than in *Aegopinella pura* and the whorls are less rounded above. Both *N. hammonis* and *N. petronella* have been described from British Postglacial deposits (Kennard & Musham, 1937; R. C. Preece, unpublished). There has been much discussion on their specific distinctness but in a recent study Waldén (1966) upholds their separation both on the basis of colour (*hammonis* is usually brownish, *petronella* always colourless or pale greenish) and consistent biometric differences.

*Oxychilus cellarius*. Plate 16, Fig. 3a, b; *Oxychilus alliarius*, *Aegopinella nitidula*. Plate 16, Fig. 4a, b; *Aegopinella pura*. Plate 14, Fig. 4a, b.

British fossil *Oxychilus* can be distinguished from *Aegopinella* by their whiter, polished, almost porcellaneous shells (glossy rather than waxy), virtual lack of spiral sculpture and differences in the umbilical characters. In juvenile *Oxychilus* the shallow umbilicus is very small and central, that of *Aegopinella* larger and strongly eccentric. When viewed from above, the outline of very young *Oxychilus* is sometimes irregular; this seldom occurs in *Aegopinella*. The suture of *Aegopinella* is deeper than in *Oxychilus*.

Juvenile *Oxychilus alliarius* can be distinguished from *O. cellarius* by its smaller protoconch, slightly more raised spire and sometimes darker colour.

Juvenile *Aegopinella pura* differ from *A. nitidula* in their tighter coiling and more keeled periphery. The reticulate microsculpture is much coarser than in *A. nitidula* and is characteristic (Plate 14, Fig. 4a, b).

*Zonitoides excavatus*.

Among the Zonitidae, adult *Z. excavatus* are distinctive because of their tight coiling and very wide umbilicus. Juveniles are harder to detect: the transverse growth ridges are often rather coarse, a feature which coupled with the wide umbilicus and lack of spiral microsculpture, can be used to separate them from *Aegopinella pura*. Immature *Z. excavatus* can resemble young *Discus* at the stage before ribbing begins, but can be distinguished by the deeper umbilicus and shallower sutures.

*Zonitoides nitidus*.

Fossil *Z. nitidus* often retain the brown gloss of living specimens and appear as if varnished. Where this gloss is not preserved the lack of a spiral microsculpture can be used for separation from *Aegopinella nitidula*. In addition, the whorls of juvenile *Z. nitidus* have a characteristically shouldered profile.

*Euconulus* spp. Plate 13, Fig. 6a, b.

*E. fulvus* and *E. alderi* are both common species in British Postglacial deposits. The latter is generally smaller with a darker shell and has more pronounced spiral microsculpture around the umbilicus (Kerney & Cameron, 1979, p. 148). However the critical differences have not been firmly established and there is much geographical variation (Dr. C. R. C. Paul, personal communication). The very fine transverse and spiral apical microsculpture is exceedingly regular and quite diagnostic of *Euconulus*.

Clausiliidae. Plate 16, Figs. 7–9.

The separation of fragments of these sinistral snails is often very hard, not only because of their similarity but also because the apices often become worn in life. The apices of the four species



commonly encountered in British Postglacial deposits decrease in size as follows: *Cochlodina laminata*, *Macrogastra rolpheii*, *Clausilia bidentata*, *Balea perversa*. *Balea* apices are distinctive not only on account of their small size but also because of their markedly conical form. Apertural fragments, which are readily identifiable, should give a clear idea of what species are present. Colour and texture of shells may help. *Cochlodina* fragments are generally cream-coloured and smooth; those of *Balea* are often buff and wrinkled rather than ribbed; while those of *M. rolpheii* and *C. bidentata* are dark (often rather reddish) and finely and regularly ribbed. The sculpture of *M. rolpheii* tends to be coarser and more prominent than in *C. bidentata*. Good reference material is really essential for naming clausiliid fragments.

*Ashfordia granulata*. Plate 13, Fig. 1a, b.

When juvenile can be distinguished from *Trichia* by its more swollen, bulbous protoconch, more obvious and regular hair pits and generally more conical shell. The umbilicus is also markedly narrower. A stereoscan photograph of the surface of a modern shell with the periostracal hairs is given by Bishop (1976).

*Zenobiella subrufescens*. Plate 15, Fig. 12.

The shell is extremely thin and feebly calcified and as yet no adults have been found fossil. Half-grown shells differ from *Trichia* and *Ashfordia* in their more tightly coiled protoconch. Unlike *Ashfordia*, *Zenobiella* lacks hair pits. The shell surface is generally rough and possesses irregular spiral and transverse sculpture. The tightness of the coiling is intermediate between that of *Aegopinella* and *Trichia*. Juveniles have a rather matt surface, but faint traces of the spiral microsculpture can still be seen.

*Trichia hispida*. Plate 13, Fig. 2a, b; *Trichia striolata*. Plate 13, Fig. 3a, b.

*T. striolata* has a slightly larger protoconch than *T. hispida* and fewer hair pits on the initial whorls but there is much variation and specimens below c. 2 mm are virtually impossible to name with confidence. An account of the formation and regeneration of hairs in *T. hispida* is given by Kaiser (1966). Half-grown shells of *T. striolata* may possess relatively strong transverse ribbing unlike *T. hispida*.

*Helicigona lapicida*. Plate 14, Fig. 2a, b.

The protoconch is smaller than that of *Cepaea* or *Arianta*. The shagreen-like microsculpture of even tiny fragments is diagnostic. Lip fragments are white, sharply reflected and also distinctive.

*Cepaea nemoralis*. Plate 14, Fig. 3; *Cepaea hortensis*.

These are the largest apices likely to be found fossil (except for those of *Helix aspersa* and *H. pomatia* in Roman and post-Roman deposits). The separation of the two *Cepaea* species when juvenile is virtually impossible. Great care must also be used when naming adult shells because the incidence of white-lipped *C. nemoralis* is particularly high in some fossil populations (Cain, 1971). Many populations of *C. nemoralis* from the early Postglacial are also entirely bandless, whereas *C. hortensis* are predominantly five-banded (Currey & Cain, 1968; Cain, 1971). The presence of banding can therefore be used as an identification guide at certain sites.

*Arianta arbustorum*. Plate 14, Fig. 5.

Well-preserved shells have a tortoiseshell colour pattern, usually with a peripheral band. The lip is white and sharply reflected at right angles. The shell fractures in a characteristic manner with many rectilinear breaks reminiscent of a broken eggshell. The surface also bears a series of wavy sub-parallel spiral grooves which appear after about the 2 whorl stage. These grooves are generally absent in *Cepaea*. Similar sculpture can be observed in the continental species *Bradybaena fruticum* (Ložek, 1964, Pl. 30, Fig. 3) which in Britain is known fossil only from interglacial deposits of Ipswichian age.



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## REVIEWS

*Hawaiian Marine Shells*. By E. Alison Kay. Published by The Bishop Museum, Honolulu, 1979. 654 pp. 195 figures, mostly photographs, 11 in full colour. Price (cloth bound) U.S. \$30.00.

*Hawaiian Marine Shells* is part IV of a projected series of six volumes on the marine fauna of the Hawaiian Islands. It stands complete and self-contained for those uninterested in phyla other than mollusca.

The opening list of contents gives the pagination for taxa from class down to sub-family. The introduction of 30 pages gives a concise and interesting outline of the Hawaiian Islands, their shore lines, types of molluscan habitats, fossil history, general composition of the marine molluscan fauna, and an historical review of the collecting and recording of this fauna as well as of the people involved. Some 550 pages then cover the species found in Hawaii, giving a good description of each, where usually found, depth range and its geographical range if beyond the island group. The figures, mostly photographs, each are of a number of species. These are generally good, although their black background is not always ideal. The author makes good use of keys and line drawings when helpful. Some 40 pages are devoted to the literature cited, listed alphabetically under authors and with dates, and finally there is an index. The book is very well produced and should stand up well to the considerable handling it will undoubtedly receive from many of its owners.

Of all the books on the molluscan fauna of a particular area, I have always thought that there is none that deserves to stand even on the same shelf as Myra Keen's 'Sea-Shells of Tropical West America'. Now at last that book can have a companion on that shelf. I cannot give Miss Kay's book higher praise.

Conchologists and collectors, tyros and old-hands alike, will I believe, find this book interesting as well as helpful. Not that, as any 'shell books', it is without its errors or scope for criticism. For example in figure 79 on page 224 items A and B have somehow been mixed up, as also have items E and F. The only criticism I would make, is that I should like to have seen more synonyms given.

Finally it should be pointed out that the book is not inexpensive, though perhaps not perhaps in view of the amount of information it contains. The latter is of course somewhat limited for those interested in a wider orbit than Hawaii, since the molluscan fauna of those islands is, as the publishers acknowledge, 'the most isolated and attenuated' in the Pacific.

A. P. H. OLIVER

*An atlas of the non-marine Mollusca of the Isle of Wight*. By R. C. Preece. 41 pp., 118 distribution maps. Isle of Wight County Museum Service, Natural History Series no. 1; Isle of Wight County Council, 1980. ISBN 0 906328 09 8. Price £2.75.

This atlas is the first to show molluscan distributions by tetrads ( $2 \times 2$  kilometre grid squares), an approach pioneered by the botanists. About 120 tetrads cover the Isle of Wight. Although the smallest English county, it is unusually varied in its geology and physiography and detailed mapping was therefore expected to reveal interesting relationships, obscured by the relatively coarse units (10 km squares) used in the national *Atlas*. This has indeed proved to be the case.

The work includes (a) an introduction describing the geology, physical features, climate and vegetation of the island, accompanied by maps showing these factors; (b) a history of research on the Mollusca from 1860 onwards; (c) the recording strategy adopted by the author; (d) changes in the molluscan fauna; and (e) critical notes on selected taxa. There is a bibliography and an index. The distribution maps, very clearly printed at eight to a page, distinguish old (pre-1950) from recent records. Though much early information, both published and unpublished, has been incorporated, the great bulk of the tetrad records (over 4,000) were gathered in an intensive field campaign in 1978-79. The maps have two unusual virtues. First, since a deliberate effort was made to cover the whole island evenly, without strong bias towards potentially rich or poor tetrads, the resulting patterns may be accepted as showing real distributions. Secondly, the brevity of the recording campaign means that we are offered a quite exceptional picture of animal populations virtually within a single season. This is clearly of great importance for the monitoring of future change. And changes are certainly occurring. For example, it is alarming to notice that the old calcareous grassland species *Helicella itala* may well be extinct in the island: though past records exist at numerous places, only occasional dead shells can be found. Conversely, several species, mostly those favoured by waste ground and gardens, are spreading. The value for conservation purposes of such precise knowledge is evident. Many of the maps also raise interesting questions about



## REVIEWS

habitat requirements and about interrelationships between species (note, for example, the curiously different distributions of the two *Cepaea* species).

The atlas is attractively printed and is in every way a model of its kind. Indeed it is the sort of publication which it is hoped other regional biological record centres will emulate.

M. P. KERNEY

*Freshwater snails of Africa and their medical importance.* By David S. Brown. Published by Taylor and Francis, x + 487 pp. text illust. with line drawings and photographs, 19 distribution maps. 8°. London, 1980. ISBN 0 85066 145 5.

Freshwater molluscs have suffered greatly at the hands of man. Either we destroy them by polluting or damming the streams in which they live or, because some of them act as intermediate hosts to medically or economically important parasites, we attempt to eradicate them systematically. Sadly we seem to succeed in polluting the harmless species more than we succeed in controlling the parasitic diseases. It is the latter aim that has led to David Brown's excellent and thorough book, as the title implies. Nevertheless there is a great deal of prime interest to students of molluscs in the book. It is not primarily a medical text, although I am sure it will prove very useful to field and research workers who need to identify economically and medically important parasites.

After a brief introduction, the bulk of the book falls into two roughly equal parts: the systematic synopsis (sections 2 introduction and key, 3 prosobranchs and 4 basommatophora; pp. 8–248) and the remaining sections (5–12; pp. 249–433) which contain the medically significant information but a lot that is of interest to freshwater biologists and malacologists as well. The systematic synopsis starts with a key which is illustrated, so that non-specialists can recognize immediately the morphological features or taxa referred to. The illustrations briefly cover shells, opercula and anatomy. The next two sections cover the prosobranch and basommatophoran faunas, are well illustrated with line drawings, photographs and the occasional scanning electron micrograph (not stereo electron micrographs as the explanations put it) and cover 81 genera and 326 species. They include brackish water species and those from north of the Sahara Desert. At the ends of these two sections some distribution maps are given. They serve to emphasize how much in its infancy this aspect of the study of African freshwater molluscs still is.

The second part of the book includes sections on: Snails and schistosomes; Other snail-borne diseases; The biology of *Bulinus*; Snail control; Local faunas; Chemical and physical factors; Reproduction and growth and finally, Regional faunas and biogeography. It can be seen from these headings that members will find much of interest even in this more medically orientated part of the book.

This broad overview is very useful and it puts previous specialist regional studies, like those on Lake Tanganyika for example, into a continental perspective. The book is well produced and indispensable to anyone interested in African freshwater snails, as well as those to whom the medical and economic aspects are more important.

For once the illustrations of sinistral snails on the dust jacket are correct. They depict species of *Bulinus*, one of the medically most important genera.

C. R. C. P.



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GOULD, S. J. 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail, *P. (Poecilozonites)* in Bermuda. *Bull. Mus. comp. Zool. Harv.* **138**: 407–532, 5 pls.

8. Authors may obtain copies of all papers at cost price if ordered from the printers, via the Hon. Editor, when the galley proofs are returned.



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# MICROGEOGRAPHICAL VARIATION IN *LITTORINA MARIAE* SACCHI & RASTELLI AND A TAXONOMIC CONSIDERATION

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(Read before the Society, 17 January, 1981)

**Abstract:** In the intertidal prosobranch *Littorina mariae* Sacchi and Rastelli from Anglesey, Wales, there was a correlation between shell morphology and shell colour in several localities. Small (5-8 mm) and large (11-14 mm) adult shells differed in morph frequencies, lip and apex colour, and sculpturing on the periostracum, and were found in different microhabitats, the former on sandy run-off channels and the latter on exposed rock platforms. The two forms were relatively discrete over short distances where the habitats were distinct, but intergraded in all characters on intermediate habitats.

Functional aspects of this variation are discussed. These differences may represent the occurrence of several taxonomic groups within *L. mariae*.

## INTRODUCTION

A bimodality of adult shell size in *Littorina obtusata* (L.) led Sacchi (1966) to suspect the existence of two co-existing groups in this highly polytypic species. On further examination of individuals of the two length modes, Sacchi and Rastelli (1966) found that there were correlated differences in sex ratio, penis morphology, colour morph frequencies and habitat. On this basis they separated *L. obtusata* into a smaller species, *mariae* (n. sp.) and a larger species *obtusata* (L. sensu stricto). Other studies confirmed these results (Sacchi, 1969) and provided additional distinctions including radula morphology (Reimchen, 1974; Goodwin and Fish, 1977) and biochemical markers (Reimchen, 1974).

*L. mariae* occurs primarily on lower intertidal Fucaceae, usually *Fucus serratus* and secondarily *F. vesiculosus* (Sacchi, 1969). It displays extensive variation in adult shell size between localities, with small adults occurring in sheltered conditions and large adults on exposed shores (Sacchi, 1969; Reimchen, 1974; Goodwin and Fish, 1977). It also demonstrates widespread variation in colour morph frequencies; a yellow morph predominates in protected bays and a dark brown morph on exposed headlands (Sacchi, 1969; Gratton, 1969; Reimchen, 1979).

Towards the conclusion of a study on *L. mariae* and *L. obtusata*, I noticed within several localities an unusually large amount of variation in adult shell size of *L. mariae*. Samples from one site in Anglesey, Wales, displayed a bimodality in size within each of the sexes, and associated with each length mode were characteristic morph frequencies, shell sculpturing and microhabitats. Collections from other sites provided several examples of similar variability. The magnitude and direction of these differences, which occurred over a distance of several meters, were equivalent to those detected when comparing samples from sheltered and exposed shores in geographical surveys.

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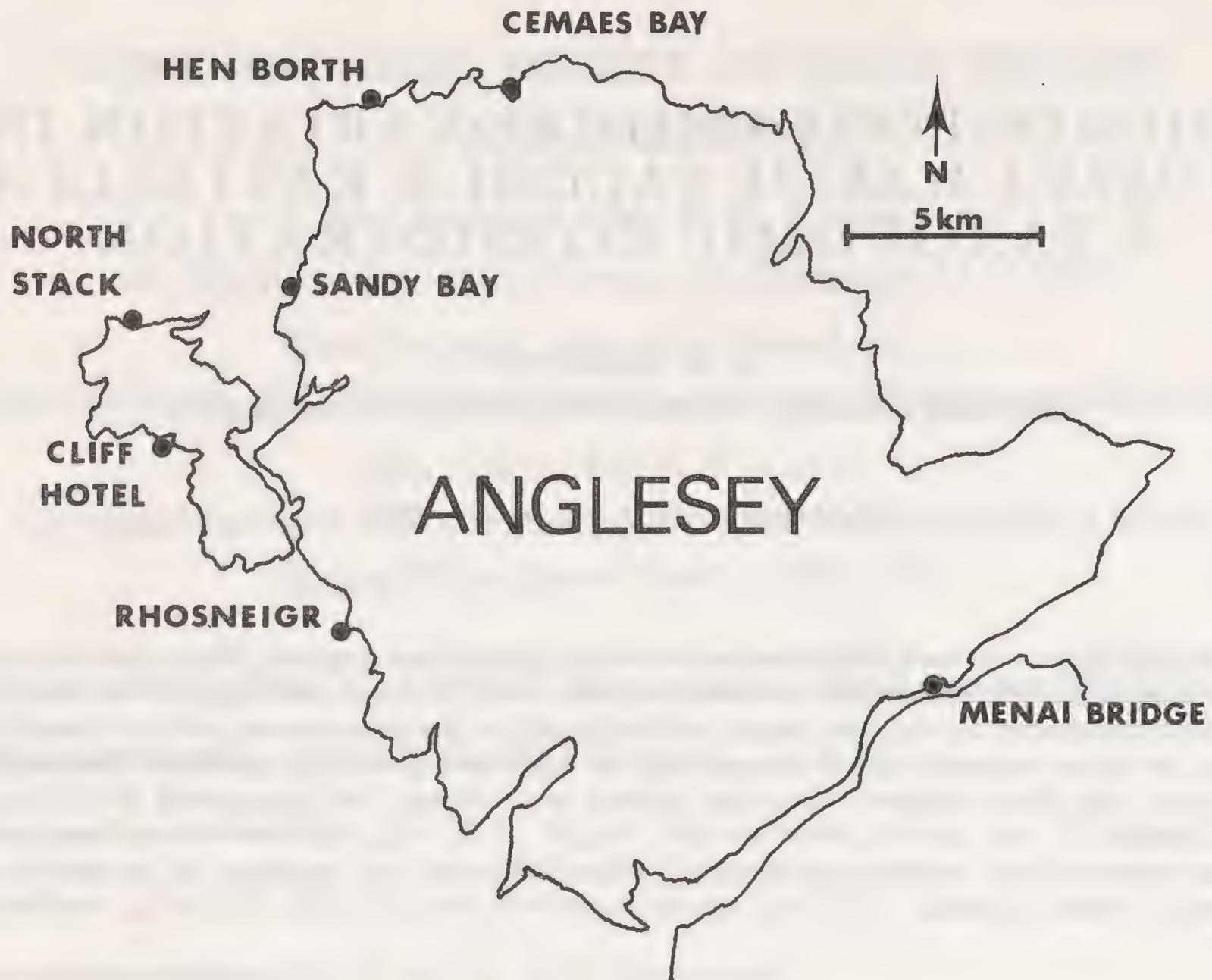


Fig. 1. Collecting areas in Anglesey, North Wales.

The purpose of this paper is to describe the microgeographical variation within these localities and to discuss briefly the possibility of a further taxonomic division within *L. mariae*.

#### STUDY AREA AND METHODS

Samples collected at Sandy Bay, Anglesey in March 1973 were used for a preliminary examination of adult shell size in *L. mariae*. This locality has a diversity of substrates including exposed bedrock platforms with modest cover of *F. spiralis*, *F. vesiculosus*, *F. serratus* and *Ascophyllum nodosum*, and sandy run-off channels with scattered clumps of *F. serratus*.

Resulting from this examination, horizontal transects were established along the shore at Sandy Bay and at 6 other localities around Anglesey (Fig. 1). These sites were chosen to include a sheltered area (Menai Bridge), a relatively exposed area (North Stack), and those with a diversity of substratum and exposure (Hen Borth, Cemaes Bay, Rhosneigr and Cliff Hotel). All snails found within a series of one meter squares were collected, first by extensive shaking of the fronds and retrieving the shells on the ground, and then by visual inspection of the fronds. Samples were preserved in 10% formaldehyde.

Adult shells, determined by the presence of a thickened lip, were measured for maximum diameter and scored for sex and colour phenotypes. In specimens from Sandy Bay, the penis was removed at the base and measured for total length and for length of the distal tubule. The major colour morphs represented were citrina, light reticulata, and dark reticulata, which correspond generally to yellow, pale brown, and dark brown respectively.

Mean adult shell size and morph frequencies from 85 localities in Ireland, Wales, Somerset, Cornwall, Devon and the Isles of Scilly were extracted from data appendices in Reimchen



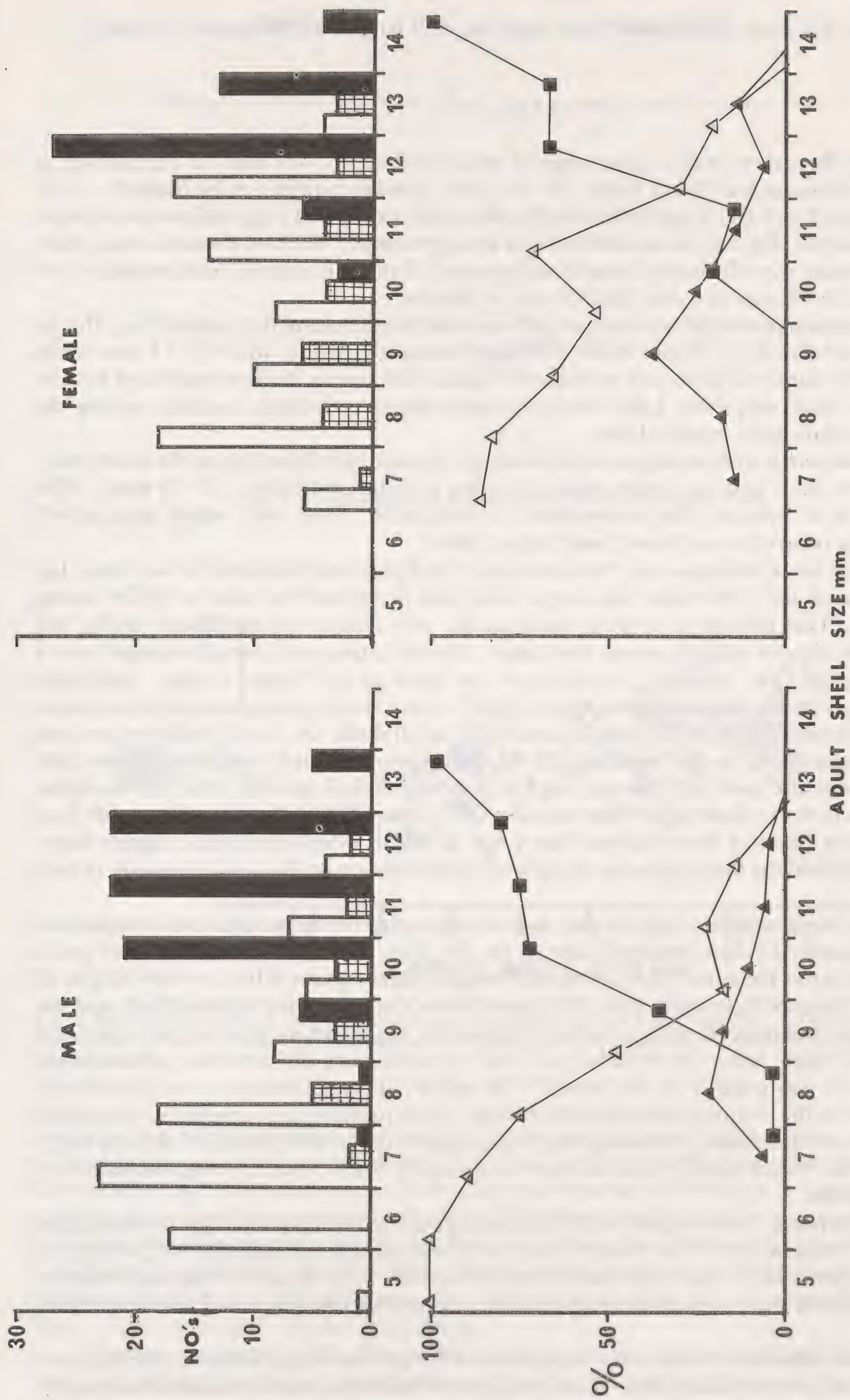


Fig. 2. A: Length distribution of adult shells from Sandy Bay among males and females for major colour morphs. Citrina—open; light reticulata—hatched; dark reticulata—solid. B: Percentage of morphs in relation to adult shell size. Citrina—open triangle; light reticulata—solid triangle; dark reticulata—solid square.



(1974). Since the sexes differ in shell size, data on shell length was restricted to males.

## RESULTS

At Sandy Bay, there was a wide range of adult shell sizes (5–14 mm) in comparison to adjacent localities such as North Stack (10–13.5 mm) (variance-ratio test for males  $P < 0.01$  and for females  $P < 0.01$ ). Length distributions for each sex showed large differences between the colour morphs (Fig. 2a). Male *citrina* had a strong mode at 7 mm and a second weak mode at 11 mm; females were distinctly bimodal at 8 mm and 12 mm. In contrast, dark *reticulata* was unimodal at 10–12 mm in males and 12 mm in females.

A correlation is present between adult shell size and frequencies of the morphs (Fig. 2b). In both males and females, 5–8 mm adults were predominantly *citrina*, while 12–14 mm adults were primarily dark *reticulata* and secondarily *citrina*. The largest shells of males and females were entirely dark *reticulata*. Light *reticulata* were disproportionately common among the morphs in intermediate length classes.

When these shells were separated into two length groups, corresponding to the lower mode of *citrina* (5–8 mm) and the upper mode of *citrina* and dark *reticulata* (11–14 mm), other distinctions were evident. For convenience in discussion, these two length groups will henceforth be referred to as 'dwarf' and 'large' forms.

There were subtle differences in the expression of shell pigments between the two forms. Lip colour in 'dwarf' light *reticulata* was tinged with pink as opposed to white or violet among 'large' shells. This phenotype graded continuously into *citrina* among 'dwarf' shells, but represented a discrete morph among the 'large'. 'Dwarf' *citrina* occasionally merged into a white phenotype (var. *albescens*), a character not seen in the 'large' *citrina*. Additional differences occurred in developmental stages of shell colour. Shell pigmentation of juveniles can generally be determined from the apex on unabraded adult shells. On 'large' shells the apex was usually the same colour as the remainder of the shell, but occasionally on 'dwarf' forms there was a discrete white apex representing the first 3–4 mm of shell growth. That this variation represents early shell colour rather than abrasion was confirmed by collections of juveniles from 2–6 mm in size. Some of the shells less than 4 mm in length were white, while slightly larger individuals showed the first expression of the adult pigmentation on the new increments of shell growth.

With low magnification (10x) one can observe sculpturing on the periostracum composed of minute longitudinal ridges perpendicular to the lip (Fig. 3). On 'dwarf' shells there was a regular series across the outer whorl, composed of high ridges separated by 2 to 4 low ridges, all about equal distance from each other. On 'large' forms the differences between high and low ridges was less pronounced, with a marked irregularity in pattern, or grading into a uniform series with all ridges being the same height. I did not detect any characteristic pattern in the 'large' form as was possible in the 'dwarf'. On adults, these differences were occasionally indistinct due to the recurrent abrasion of the shells, but in juvenile and sub-adults, sculpturing was usually well developed. At Sandy Bay, the majority of juvenile *citrina* (4–6 mm) had a pattern like the 'dwarf' adults, while all dark *reticulata* (4–9 mm) had the irregular pattern of the 'large' adults.

Minor differences were evident in the morphology of the penis, specifically, in the relative length of the distal tubule. In the 'dwarf' form, the tubule constituted about 30–40% of the total length of the penis and in the 'large' form it represented 60–70%. However, this may represent allometric growth since a continuous gradation was present between small and large snails (Fig. 4).

There were consistent trends in the abundance of 'dwarf' and 'large' forms on different parts of the shore (Fig. 5). At Sandy Bay, 'dwarf' shells were most common on isolated clumps of *F*.



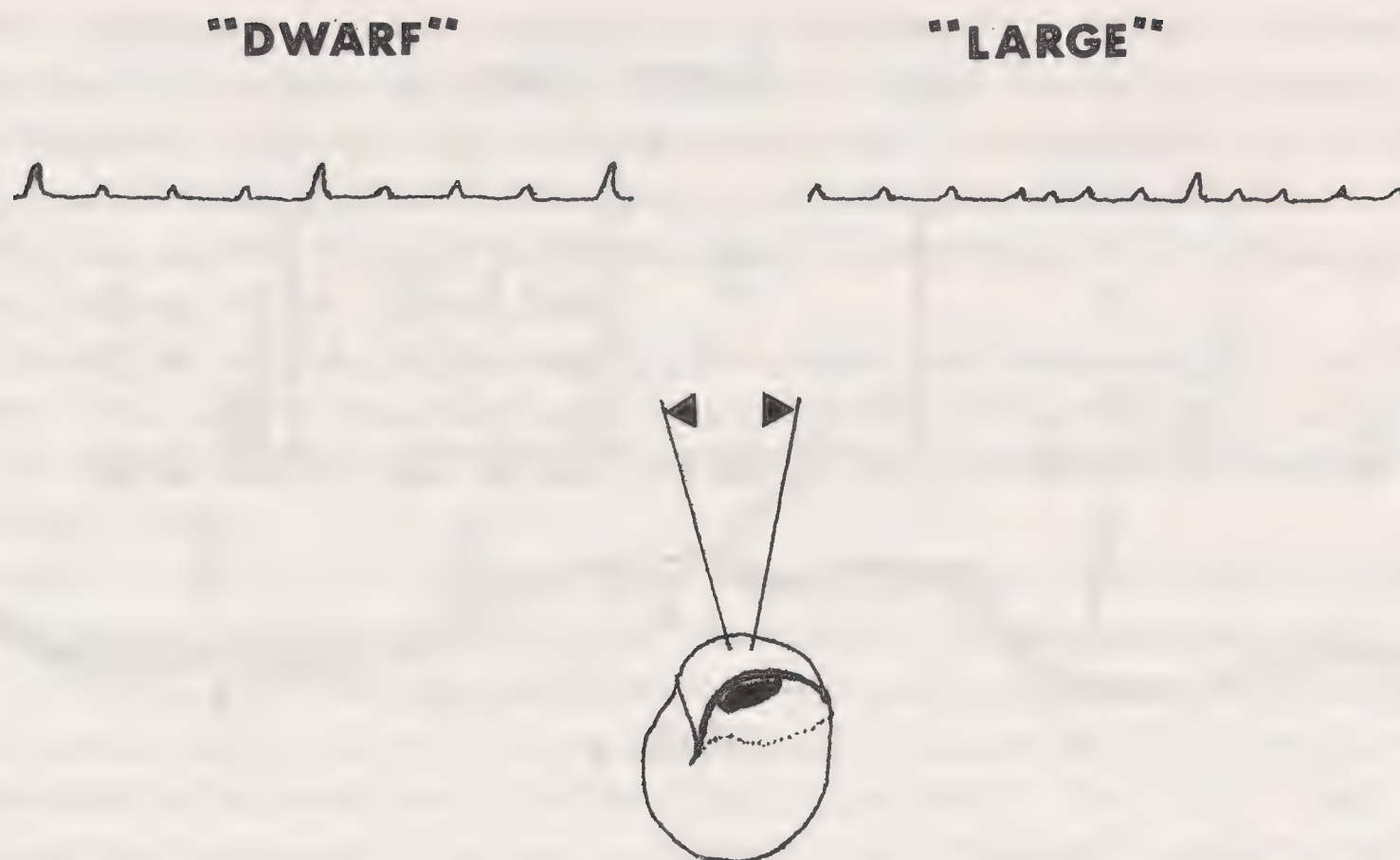


Fig. 3. Sculpturing on periostracum of 'dwarf' and 'large' shells.

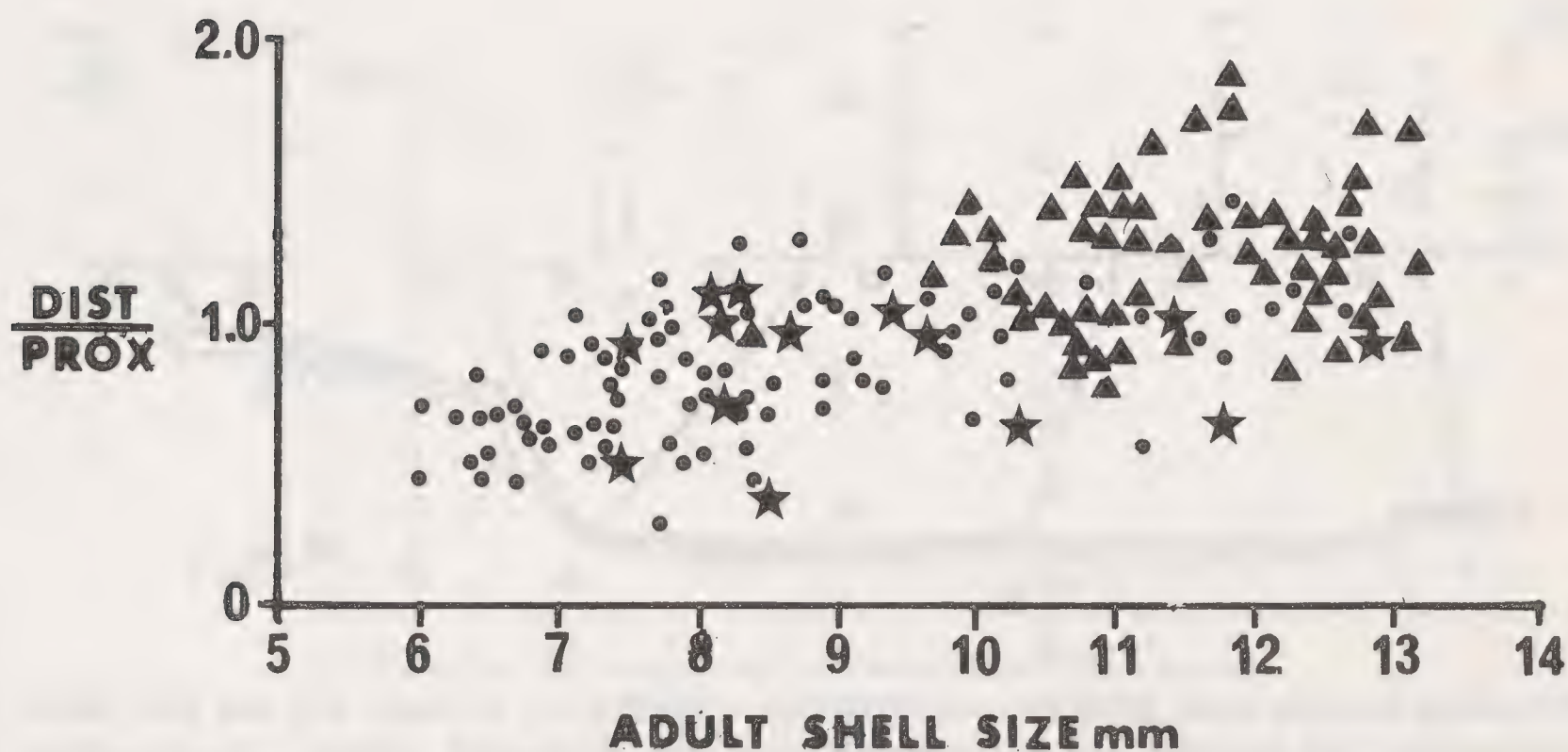


Fig. 4. Scatter plot of relative length of distal tubule and adult shell size from Sandy Bay. Vertical axis represents a length ratio of distal tubule to the proximal section. Citrina—dot; dark reticulata—triangle; reticulata with white apex—star.

*serratus* which were underlain and surrounded by sand or gravel, this habitat occurring in sheltered tidal run-off channels (site no. 5). In these areas, *F. serratus* had broad laminae, short narrow stems and often numerous tube-dwelling polychaetes (*Spirorbis* spp.). 'Large' shells were most abundant on *F. serratus* from elevated rock platforms, areas which were relatively exposed to wave action (sites no. 3 and 6). Fronds had narrow laminae, seldom with *Spirorbis*, and large broad stems which often constituted the major length of the frond. Samples from low rock platforms (site no. 1) and from intermediate areas (sites no. 2, 3 and 4) contained 'dwarf' and 'large' shells in roughly similar proportions.

There were suggestions of a length bimodality in citrina (sites no. 1, 4 and 6) and in each case, individuals from the lower mode retained the characteristic sculpturing of the 'dwarf' form



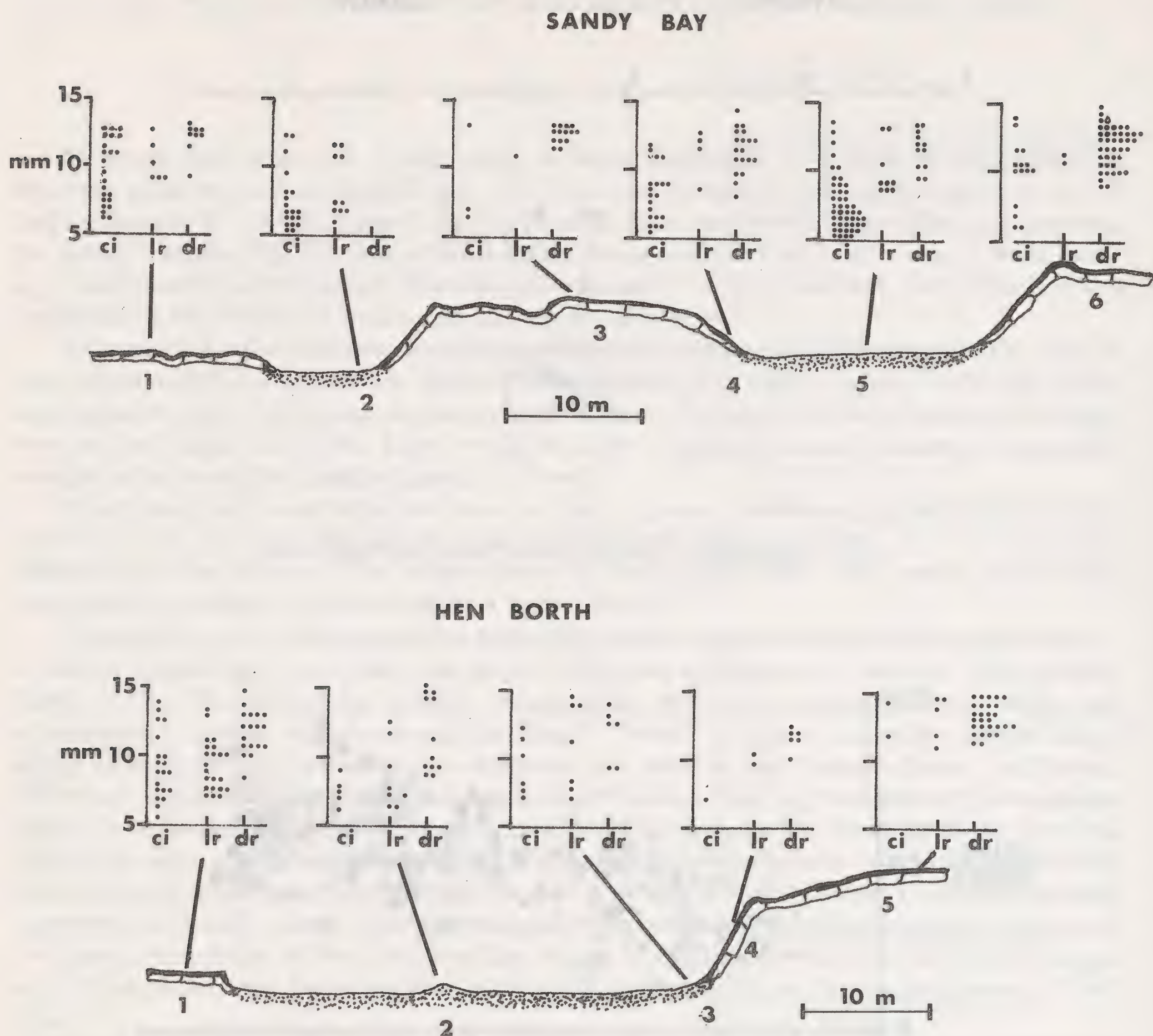


Fig. 5. Relationship between adult shell size, colour morph, and substrate at Sandy Bay and Hen Borth. Shoreline shown in cross-section with elevated rock platforms and sandy run-off channels (dotted). Graphs indicate size of all adult males in sample for each colour morph (citrina—ci; light reticulata—lr; dark reticulata—dr).

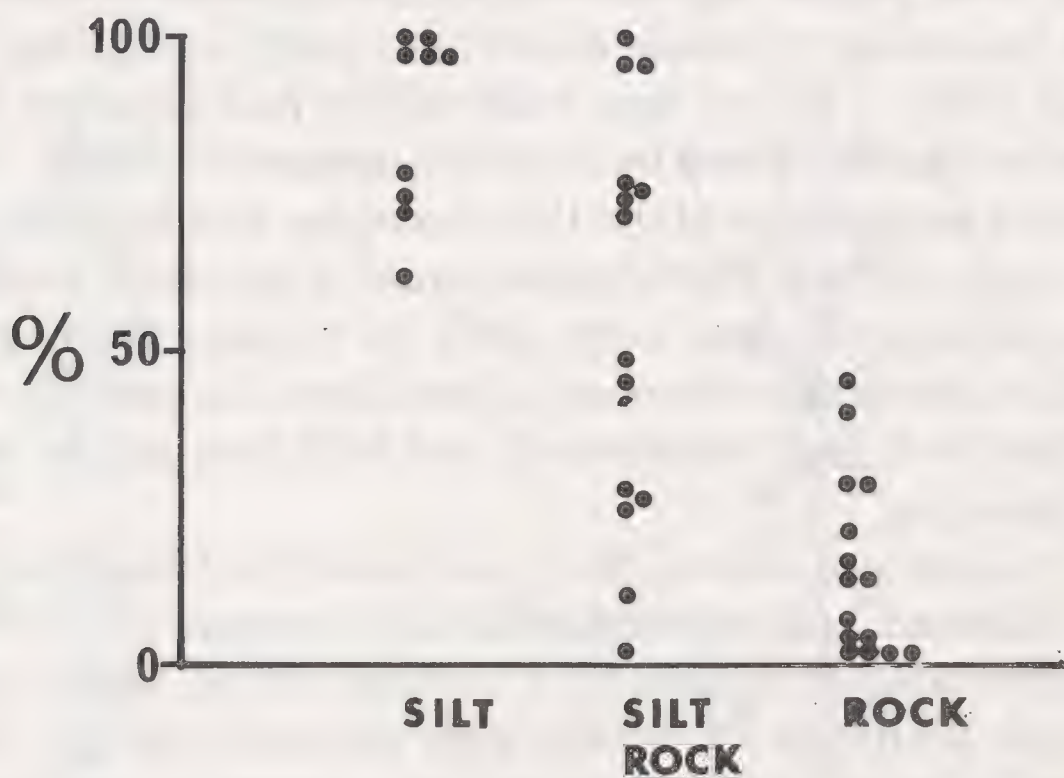
while those from the upper mode had sculpturing like 'large' dark reticulata. Light reticulata was often intermediate in size between the 'dwarf' and 'large' forms (sites no. 1 and 5). Sculpturing on these individuals was similar to the 'dwarf' form in having high ridges separated by several low ridges, yet the series was very irregular.

The trends described for Sandy Bay were also detected at Hen Borth, Rhosneigr and Cliff Hotel where there was an equivalent diversity in substrata. At Hen Borth (Fig. 5), light reticulata was again intermediate in size (site no. 1), but the smallest shells (site no. 2) and largest shells (site no. 5) had sculpturing characteristic of the 'dwarf' and 'large' forms respectively. A feature of this locality is the high incidence of the white apex. Dark reticulata phenotypes showing this character were generally similar to the 'dwarf' in sculpturing but in all of the samples, these shells were slightly larger than 'dwarf' citrina.

At Cemaes Bay, the diversity of substrata was reduced and snails were found only on several



Menai Bridge, a very sheltered locality, has a dominant substratum of loose sand and silt. Samples from this locality contained only 'dwarf' shells. At North Stack, a relatively exposed headland, the major habitat was sloping bedrock, with occasional rock shelves; all of the shells were the 'large' form.





shell length; this gave the 'dwarf' an advantage during predation by small *C. maenas* which breaks away successive parts of the outer whorl. In contrast, when adult shells were exposed to large *C. maenas*, the 'dwarf' were at a distinct disadvantage since their entire shell could be crushed by the major claw. It follows that local differences in the abundance and size distribution of crabs (cf. Ebling *et al.*, 1964; Raffaelli, 1978) will provide differing selective forces.

Differences in colour morph frequencies between localities have been interpreted as a response to visual predators such as *Blennius pholis* (Reimchen, 1979). In sheltered localities where citrina predominates, the majority of juvenile snails were found on the broad lamina of *F. serratus*. Since yellow is the dominant light transmitted through the lamina, citrina is the most camouflaged of the morphs. On exposed shores, where dark reticulata occurs, juveniles were found on the opaque brown stem of *F. serratus* where only dark reticulata is cryptic. It is unknown whether these differences between shores will apply as well to differences between run-off channels and adjacent rock platforms.

The white apex on 'dwarf' reticulata phenotypes was associated with fronds of *F. serratus* densely covered with tube-dwelling polychaetes. After hatching and during the first 4 mm of shell growth, some snails have a white-banded shell which closely resembles the white tubes of *Spirorbis*. In predation experiments with *Blennius pholis*, white shells were consumed less frequently than equivalent sized yellow or brown shells (Reimchen, in preparation).

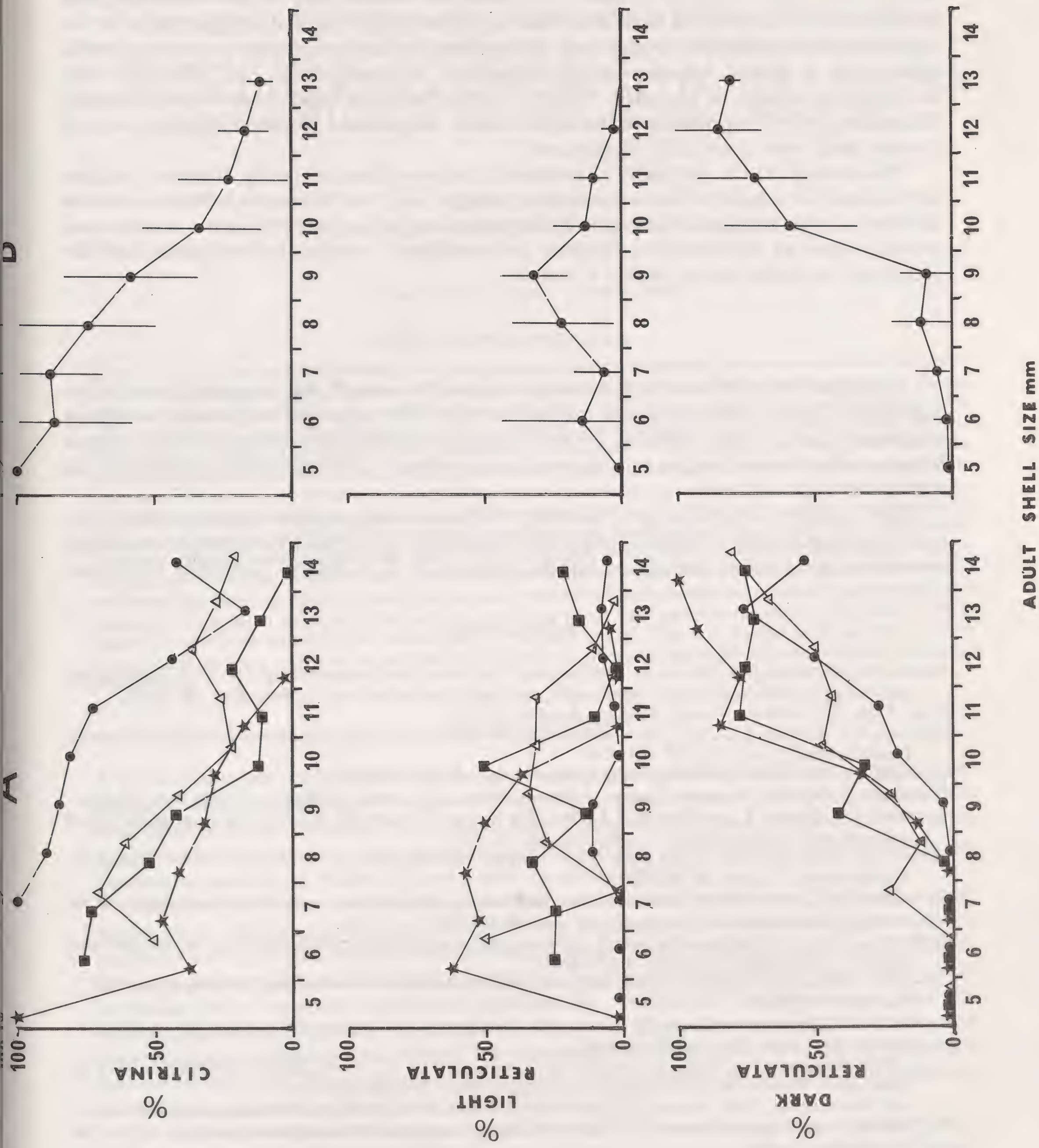
The close relationship between shell size and frequencies of colour morphs within these localities is also applicable to the general parameters of populations between localities. Using data from Reimchen (1974) involving 85 localities around Britain and Ireland, mean adult shell length in each locality was plotted against the percentage of each morph. Localities were then grouped and a mean percentage obtained from 1 mm length categories (5–6 mm, 6–7 mm, etc.). The resulting graph (Fig. 7) shows that both within and between localities the small length classes (5–8 mm) were characterized by high frequencies of citrina, intermediate length classes (9–11 mm) by similar proportions of the three morphs, and large shells (11–15 mm) by dark reticulata and secondarily citrina. Furthermore, small adult shells were found in sheltered localities, often with sand substratum, and large shells on exposed shores generally with rock substratum. When these samples were reexamined, those from sheltered shores in Ireland, Isles of Scilly and South England with small adult shells and high frequencies of citrina contained characteristic 'dwarf' sculpturing.

It is probable that the majority of these shell characters in the 'dwarf' and 'large' forms and those observed between sheltered and exposed localities represent very localized adaptation resulting, in part, from differential predation by *C. maenas* and *B. pholis*. Since sandy run-off channels and elevated rock platforms or shelter and exposure merge through a series of intermediate areas the gradation of shell characters may represent an adaptive response to 'intermediacy' in the selective regimes.

These data raise several difficulties concerning the genetic structure of the variation whereby a complex of characters can differ over several meters in a manner parallel to that of wide geographical distances. If this indicates genetic variations within a single species, it would require numerous linkage groups between adult shell size and the following characters: habitat, shell colour (bimodal in citrina, intermediate in light reticulata, and large in dark reticulata), presence or absence of a white juvenile phase, shell sculpturing, and the ability to express these characters in any complex of intermediate states according to the intermediacy of the habitat. While it is possible to incorporate a multiple-character association within a polymorphic

Fig. 7. A: Frequencies of colour morphs and adult shell size of males within localities from Anglesey. Rhosneigr (N = 59)—star; Hen Borth (N = 58)—square; Cemaes Bay (N = 80)—dot; Cliff Hotel (N = 67)—triangle. See Fig. 2 for data from Sandy Bay. B: Frequencies of colour morphs and mean adult shell size for males from localities in Ireland, Wales, Somerset, Devon, Cornwall, and Isles of Scilly. Vertical line shows one standard deviation from mean frequencies for localities with the corresponding mean adult shell size. Data from sites in Anglesey (Part A) excluded.







context (cf. Ford, 1964), the magnitude of the changes suggests a basic difference in the genome, and the occurrence of several taxonomic groups. If only two general groups are conceived, a 'dwarf' and a 'large' form, the frequent morphological intermediacy in light reticulata, both within samples and between localities, remains problematic. A second interpretation for the correlation between shell characters and microhabitat is that it represents an environmental rather than a genetic response. Until heritability is estimated for each character, this interpretation cannot be excluded. However, where breeding experiments were performed (Reimchen, 1974), expressions of the major colour morphs and the white-banded phase of juvenile shells were genetically determined.

The existing data do not justify a taxonomic division within the species. However, because of occasional bimodality in characters and very sharp clines, they do provide sufficient cause for an informal separation in further work. Multivariate analysis and electrophoretic variants may provide means of distinguishing between an exceedingly complex polymorphism and the occurrence of sibling species within *L. mariae*.

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# COMMUNITIES AND DIVERSITY OF LAND MOLLUSCS IN SCANDINAVIAN WOODLANDS. I. HIGH DIVERSITY COMMUNITIES IN TALUSES AND BOULDER SLOPES IN SW SWEDEN

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*Abstract:* In a largely non-calcareous area in SW Sweden the most diversified land mollusc communities occur in wooded talus and boulder slope habitats. There is a very strong correlation between pH and the number of snail species, whereas differences in slope aspect have a very modest influence only. Up to 34 snail species have been found co-existing in the southern slope sector, up to 29 species in the northern sector. On average there is an increase of 5 species per pH unit. Depending on the size of the sample (in the present survey standardized to 20 l), occasional collecting circumstances, and population dynamics of the individual species, all species of a site are in most cases not obtained in the same sample. An attempt to estimate the real diversity at different pH values has been made. Up to 37 snail species probably co-exist in the richest sites. The number of slug species is more difficult to assess. However, up to 7 species have been found together in talus and boulder slopes, and 6 species may be regularly present in the sites already at pH 5. Causes of the high diversity in wooded talus and boulder slopes are discussed. There is a rich microhabitat differentiation and good access to shelter, allowing survival during adverse periods. Furthermore, the study shows that when conditions improve species with a similar ecology tend to accumulate rather than replace each other. This indicates that competition is of subordinate importance. Compared with many other regions, and in particular with regard to the fairly high latitude (*c.* 58°), figures for co-existing species in SW Sweden must be regarded as high. This may depend partly on the particular geographical situation, partly on the evolutionary background, favouring species pre-adapted to a broad ecological co-existence.

## 1. INTRODUCTION

A considerable part of the land mollusc species of central and northwestern Europe reaches northern distributional limits within a relatively narrow zone in southern and middle Scandinavia. Along the coasts most species show a marked deflection northwards, in western Scandinavia for more or less suboceanic species, in eastern Scandinavia particularly for continental species (cf. maps in Kerney and Cameron, 1979).

Compared with the more densely populated and industrialized parts of Europe relatively undisturbed, original habitats are still rather well represented in Scandinavia. Although the process of habitat destruction or transformation is rapid and accelerating, there is still certainly better opportunity to study original biocoenotic conditions than in most other countries, in particular when extensive series are desirable for comparison and proving trends. An outstanding feature is that the mollusc communities sometimes show a very high diversity, and the essentially undisturbed character of these communities makes them particularly interesting and useful for study. The author's intention is to elucidate this and certain other aspects of crucial interest of the mollusc fauna, in a series of papers.

In southwestern Scandinavia the most diversified mollusc communities exist in wooded talus and boulder slope habitats. The diversity is high not only in absolute number of species, but also in percentage of the total mollusc fauna of the area. In the richest sites of this kind about 2/3 of the total number of woodland species have been found co-existing. The purpose of the



present paper is to throw light on how diversity depends on topographic, trophic (represented by pH), and local climatic (depending on the aspect of the slope) factors, to give characteristic examples of mollusc communities in relation to these factors, and to discuss possible reasons for the high degree of co-existence among molluscs.

## 2. AREA OF INVESTIGATION

The present study is based on material from a continuing extensive survey on distribution, ecology and geographical variation of terrestrial gastropods in Sweden (cf. Waldén, 1965). The area in southwestern Sweden, from which the material originates, is shown on the map (Fig. 1). The samples were collected during the years 1961–1979.

Disregarding plains and valleys with marine sediments, the area is largely oligotrophic. The climate is humid, and the area includes parts with the highest rainfall ( $> 900$  mm/yr) in southern Scandinavia. Towards the coast, precipitation declines (locally to  $< 600$  mm/yr), but the climate becomes increasingly maritime, with high relative humidity.

The bedrock is predominantly composed of acid gneisses, in limited areas granitic. However, in the northern parts, bedrock occurs which is more favourable from a trophic viewpoint, consisting of basic intrusives, partly overlying Palaeozoic sedimentary strata, greenstones, relatively calcium-rich schists etc. (the Precambrian Dal Formation). These outcrops have considerable influence on the abundance and diversity of molluscs. Here the highest numbers of co-existing species have been encountered.

With very few, local exceptions the boulder slope habitats are entirely devoid of calcium carbonate. Only certain soils contain free  $\text{CaCO}_3$ , viz. moraines (in deeper, non-leached levels only) in the southernmost parts, derived from Cretaceous or Palaeozoic strata, and marine shell sand, mainly in the province of Bohuslän. Here it can sometimes occur between boulders, or in subsoil under the boulder slopes, as a consequence of the post-glacial submergence. Evidently this contributes to the presence of certain fastidious species and partly explains the generally higher diversity in the northern part of the study area.

The landscape is largely hilly, passing over to the higher and flatter central peneplain of southern Sweden. Steep rock slopes and cliffs, which form pre-conditions for developing taluses and boulder slopes, are widespread from the coast and inwards along fissure zones and river valleys. Particularly well developed taluses are present at table mountains, where dolerite layers with lofty, vertical cliffs rest upon untilted Palaeozoic strata. Some of the richest mollusc communities occur here (examples are site 9 in Table 3 and site 13 in Table 4).

Ancient woodland, sometimes of an almost virgin character, has been preserved to a greater extent in taluses and boulder slopes than in any other habitat, certainly owing to their relative inaccessibility. This is of decisive importance for the survival of certain stenoecious species and for maintaining high-diversity mollusc communities in general.

## 3. MATERIAL AND METHODS

The survey is based on standardized samples of litter, mosses etc. of *c.* 20 l volume. The samples are dried and separated by sieving into fractions of different particle size, from which the shells are extracted by hand-sorting. The finest fraction is sorted under a magnifying glass. This extraction method is very time-consuming, but highly exhaustive and less biased than any other method.

This is most important with regard to the accuracy of numbers for minute species and indeed, the juveniles. Nevertheless, substantial losses of juveniles cannot be avoided for the smallest forms, such as *Vertigo*, *Punctum* and *Carychium*. The losses are estimated to be, in most



cases, between 5–20% of the real numbers of respective species. For only slightly larger forms, such as *Cochlicopa* and *Nesovitrea*, extraction is fairly good even for the smallest juveniles, and the losses may be only a few per cent of the numbers for the respective species.

The samples were not taken from a standardized area, but the area from which substratum for sifting was gathered seldom exceeded  $100 \times 100$  m; often it was considerably less. The main criterion is that the habitat should be reasonably homogenous; form and size of the sampling area being of subordinate importance.

Sampling was not random, but the aim has been that the material gathered should reflect the composition of the habitat. However, the quantitative results probably do not deviate very much from those which would have been achieved by a strictly randomized sampling. The method used e.g. by Wäreborn (1969, p. 462) is nearly identical, even if standardized in a slightly different manner. No doubt a comparison of results is feasible.

Litter sieving was supplemented by direct picking of snails, mainly in micro-habitats not available by the former method (under logs, on boulder surfaces etc.), and also by shaking or sweeping the vegetation with a catcher. A primary goal was always to detect the species of the site as exhaustively as possible. Of course the adding of directly collected specimens affects the figures for dominance (relative abundance) between species, but on the whole the effect can be considered marginal. These cases are marked by an asterisk in the tables.

Slugs were recorded by direct gathering or observation. These results do not allow proper comparison; only a rough estimate of the slug fauna under different conditions is possible (cf. comments in section 9).

pH has been used as an ecological parameter, measured colorimetrically on small samples from the sifted litter (using S.K.P. Soil Tester, Weibull Ltd). According to Wäreborn (1969, p. 463) the values obtained deviate at most by 0.25 units from values determined with a standard glass electrode. Usually two pH tests were made per sample. On samples from somewhat heterogeneous habitats four or more tests were made.

In 50% of the samples there was no difference at all between the tests. In less than 4% the difference was between 0.75–1.00 pH units, and in the rest between 0.25–0.50 units.

#### 4. SAMPLE SIZE AND DIVERSITY

Some attention must be devoted to how the size of the sample may affect the number of species indicated. It is empirically well established that provided that the ecological conditions—including degree of microhabitat differentiation—are reasonably alike, the number of species in land mollusc communities is a function of the number of specimens, this being the basic variable (cf. discussion in Fisher *et al.*, 1943). Except in some extreme cases when density-dependent factors and patchiness may interfere, or when large, usually low-density species (such as *Cepaea* and *Arianta*) are involved, the size *per se* of area or volume from which a particular number of specimens has been extracted has very little effect on the number of species. Conversely, larger quantities of substrate must be examined when the density of individuals is low, in order to sample rarer species.

The mathematical relation between number of species and specimens could not be considered here. But it can be stated that in contrast to the major groups of flying insects (cf. examples in Fisher *et al.*, 1943) a definite limit to the number of species in a habitat is reached rather soon, for poor mollusc communities perhaps already at the level of a few hundred specimens. In the case of very rich communities no further species would probably be expected at a level of some 10,000 specimens.

No generally accepted theoretical definition of 'minimum sample size' (corresponding to the 'minimum area' of plant ecologists) when the 'constant' or 'characteristic' species will be



represented, has been achieved. At least for molluscs, however, this implies no significant practical problem. Species which may be lacking in 'minimum size' samples are usually ecologically marginal or alien, and can be empirically distinguished by the experienced molluscan ecologist. The samples on which the present study is based mostly well fulfil the condition of 'minimum size'. Crucial cases will be considered in section 10, concerning the probable upper limit of co-existing species in habitats.

## 5. RICH AND POOR WOODLAND HABITATS

It is generally recognized that topography, besides pedochemical factors, climate and vegetation, has considerable influence on the diversity of land molluscs. Causes of this will be discussed later. Here an empirical estimate should be made on the potential mollusc diversity under different topographical and gross habitat conditions.

The estimate is made on the basis of the material of investigated woodlands in Halland province, where the mollusc fauna has been fairly exhaustively surveyed (Waldén, 1969). A grouping of the results is made in Table 1. Only material from the survey by the present author (1961–68) has been used, because these data are associated with pH records, and consequently relevant in the present context. The previous material of Lohmander (cf. Lohmander, 1923, 1960), largely of the same size and composition, gives an essentially consistent impression, except that it is not supported by pH data.

Less important woodland types (dominated by trivial trees such as birch and aspen) will not be considered. Of the coniferous woods only those with some intermixture of deciduous trees or bushes are included. Pure stands of pine or spruce seldom house more than 3–4 snail species and a few slugs. Coniferous woods with a richer intermixture of deciduous trees, on the other hand, have a fauna converging on that of corresponding deciduous woods (oak-dominated, beech-dominated etc.).

*Comments on table 1.* The grouping of habitats in the table is rough, but nevertheless the general trend is quite striking. By far the richest habitat in Halland is the broadleaf forest on calcareous moraine; this in itself is scarcely surprising. However, the mollusc diversity here is somewhat exaggerated in the material, because this habitat is more heterogeneous than the other ones. A typical calcareous ravine habitat has a brook or swampy ground in the bottom, and therefore typical wet ground species such as *Succinea putris* (L.), *Euconulus alderi* (Gray) and *Carychium minimum* Müll. are regularly present.

Next to broadleaf forests on calcareous moraine, the talus and boulder slope habitats have the richest mollusc communities, independent of the kind of woodland. This is the more striking as they are, with very few exceptions, situated on poor gneissic bedrock, with a moderate or low pH in the förna layer.

Considerably higher numbers of mollusc species are found in boulder slope habitats locally in the provinces of Bohuslän, Dalsland, and Västergötland, associated with the outcrops of basic intrusives, Precambrian schists etc. (cf. section 2). All the examples of high-diversity communities in the tables emanate from there, and clearly surpass the numbers known from habitats on calcareous soil. In Bohuslän up to 24 testaceous species (and 5 slug species) have been recorded from damp deciduous wood in ravines in shell sand. Interest therefore will be concentrated on the talus and boulder slope habitats.



TABLE 1

Number of snail and slug species found in woodlands in Halland (SW Sweden)  
(Except for the broadleaf woods on chalk moraine, all localities are non-calcareous, acid to circum-neutral)

| Gross habitat                                                      | Number<br>of<br>sites | pH      | Snails            |      | Slugs                                                  |
|--------------------------------------------------------------------|-----------------------|---------|-------------------|------|--------------------------------------------------------|
|                                                                    |                       |         | Number of species |      | Maximum number of<br>species found in<br>the same site |
|                                                                    |                       |         | Amplitude         | Mean |                                                        |
| Coniferous wood                                                    | 3                     | 4.5–5.0 | 4–7               | 5.7  | 6                                                      |
| Oak wood                                                           |                       |         |                   |      |                                                        |
| I. On flat or slightly<br>broken ground                            | 4                     | 4.5–<6  | 6–13              | 9.0  | 5                                                      |
| II. On sloping ground,<br>sometimes moderately<br>rich in boulders | 26                    | 4.5–7.0 | 5–17              | 10.5 | 6                                                      |
| III. In taluses and<br>boulder slopes                              | 7                     | 5.0–>6  | 8–20              | 13.4 | 7                                                      |
| Beech wood                                                         |                       |         |                   |      |                                                        |
| I. On flat or slightly<br>broken ground                            | 4                     | 5.0–5.5 | 6–14              | 10.8 | 5                                                      |
| II. On sloping ground,<br>sometimes moderately<br>rich in boulders | 26                    | >4–>6   | 4–14              | 10.2 | 6                                                      |
| III. In taluses and<br>boulder slopes                              | 6                     | 4.5–6.5 | 11–22             | 15.2 | 7                                                      |
| Luxuriant broadleaf wood                                           |                       |         |                   |      |                                                        |
| I. On calcareous moraine<br>(mainly ravines)                       | 5                     | 6.0–>7  | 24–27             | 25.2 | 8                                                      |
| II. In taluses and<br>boulder slopes                               | 2                     | <6–7.0  | 17                | 17.0 | 5                                                      |

6. HABITAT CRITERIA AND MICROHABITATS

Habitats with high species diversity are composite, either obviously by their topographical and vegetational structure, or more or less concealed, as when a mosaic of ecological niches occurs. Our present knowledge is not sufficient to allow a decision as to what extent terrestrial gastropods can co-exist in the same ecological niches, but available evidence suggests that there is considerable overlap, plasticity in food choice, and that competition is not a critical factor in northern woodland habitats. However, when dealing with ‘communities’, in the meaning of the fauna of a particular animal group represented within a habitat, it is essential to specify how the habitat is delimited.

In the present study on talus and boulder slope habitats, the following criteria are applied:  
(1) Topographically: the slope is steep and covered by boulders and stones. In most cases this is due to talus formation, often still active. Alternatively, the boulder slopes may be of moraine origin or due to abrasion during a former submergence stage. In these cases boulders and stones are usually more or less rounded by wear. It should be noted that on at least part of the slope the cover of boulders and stones is closed, often in deep layers with a consequent extensive system of interstices. Furthermore, all the sites selected for the present study—not only the taluses—are characterized by the presence of bedrock above the boulder slope, usually a precipice.



(2) Rocky cliffs above, and soil slopes below, the boulder slopes fall beyond the scope of this study, though transitional zones with more scattered boulders may be included. The presence of certain species, ecologically atypical for the boulder slopes may be included. The presence of certain species, ecologically atypical for the boulder slopes, may depend on such adjacent habitats.

Andersson (1961, pp. 127–129) gives an account of the structural and physiognomic features of talus habitats in northern Sweden. This is largely valid for talus habitats in southern Sweden too, though the hills are usually of smaller dimensions and the deciduous vegetation richer and more varied. Another type, with less prominent boulder slope and closed vegetation contour, is shown in a scheme by Wäreborn (1969, Fig. 4). The latter author also considers the moisture pattern.

(3) Vegetation strata are in a more or less natural state; profoundly altered sites are thus excluded from the study. Indeed, it is in talus and boulder slopes that original woodland has the best chance to survive, owing to their relative inaccessibility, or at least unsuitability for forest exploitation. Usually, though by no means generally, the wood is most closed in the uppermost and the lower part of the slope. In the middle, trees may be sparser or even absent, owing to lack of fine material to grow in. Such open zones, and adjacent wood margins, form very particular subhabitats, apparently of importance for the diversity of the mollusc fauna.

(4) The wood is prevailingly deciduous, though at lower pH conifers become increasingly dominant (except in the coastal areas, where natural coniferous wood does not occur). However, in the present material there is at least some intermixture of deciduous trees, which are of definite importance for producing a litter suitable for molluscs. Indeed, deciduous trees are almost invariably present in undisturbed boulder slopes and can be regarded as ecological constituents. When lacking, this is almost always caused by felling.

(5) Patches with meadow vegetation (on soil) as well as wet ground—for example along brooks and springs—may occur in connection with talus and boulder slopes, but support a partly quite different fauna. This element is therefore excluded from the study.

*Microhabitats.* Within the ecological framework, circumscribed here, talus and boulder slopes exhibit usually a decided mosaic of microhabitats, because of the system of interstices, boulder surfaces at every inclination, the accumulation of litter of varying depth, moisture and decomposition etc. Vegetation may be diverse or relatively uniform, but in both cases it tends to have a mosaic character, and contributes to diversity in shadyness/sun exposure, dampness/dryness, and other microclimatic features. In addition, the slope situation itself is climatically favourable, with regard to insolation angle, thermal inversion and low frost exposure. Even if the vertical zonation with regard to microclimate and vegetation is important—and, indeed, some species (e.g. *Lauria cylindracea*) tend to be concentrated to narrow zones—a striking feature of talus and boulder slopes is that a great microhabitat diversity can be displayed within very small areas.

As mentioned in section 3, the samples on which the present survey is based emanate from areas which seldom exceed 100 × 100 m.

In addition to the actual microhabitat diversity, the boulder topography gives shelter during adverse periods. After felling, considerable bush vegetation may persist between boulders, sprouting from deciduous tree stumps takes place, and the temporary transformation of the habitat will not be as complete as in a more open terrain. The mollusc community will have a relatively good chance of survival under the fragmentary vegetation and in interstices. This implies a better balance between persistence and addition of species on the one side, and losses on the other, and may in the long run contribute to maintaining a high level of diversity in talus and boulder slope habitats.



## 7. ON THE TOTAL STOCK OF SPECIES, WITH SOME ECOLOGICAL AND TAXONOMICAL REMARKS

In all 49 testaceous and 14 slug species are known to occur in talus and boulder slope habitats in the area surveyed (Fig. 1). In addition to those listed in the tables 2, 3, and 4, the following have also been recorded:

*Succinea oblonga* Drap.

*Vallonia pulchella* (Müll.)

*Vallonia excentrica* Sterki

*Truncatellina costulata* (Nilsson)

*Clausilia dubia* Drap.

Some species are extremely rare in these habitats, either because their ecological requirements are extremely narrow, or because they are not typical for the habitat and their occurrence there is more or less accidental. The latter cause may be complicated by the fact that some species are on the edge of their distribution, without necessarily giving an obvious impression of being ecologically selective. Among the alien species, the pronounced synanthropes form a characteristic group. To conclude, the following species can be placed in these somewhat heterogeneous categories:

*Succinea putris*

*S. oblonga*

*Truncatellina costulata*

*Vertigo pygmaea*

*Vallonia pulchella*

*V. excentrica*

*Zoogenetes harpa*

*Arion hortensis* auctt.

*Limax maximus*

*Deroceras laeve*

*D. reticulatum*

*Clausilia dubia*

*Trichia hispida*

*Ecological remarks:* The occurrence of the hygrophilous *S. putris* and *D. laeve* in boulder slope habitats seems to be peculiar to humid SW Sweden. In other parts of the country they are confined to damp or wet habitats. However, most probably their reproduction sites are on damp ground at the foot of the slopes, and they may occur in the slopes merely as active wanderers under humid conditions.

Boycott (1934) classifies *S. oblonga* and *V. angustior* as obligatory hygrophiles. However, in Sweden both occur normally in drier conditions as well. Indeed, *V. angustior* is a quite characteristic inhabitant of certain types of talus and boulder slopes (cf. Table 3), in particular near the coast.

*Taxonomical remarks:* Nomenclature follows Kerney and Cameron (1979):

The occurrence of intermediate forms of *Cochlicopa* in some tracts, which cannot be assigned unequivocally to *C. lubrica* or *lubricella*, has not yet been satisfactorily explained. Possible causes of this should not be discussed here, but attention should be drawn to the fact that there seems to be a considerable phenotypic variation in both species, which may to some extent depend on differences in rainfall between years. Intermediate specimens are not uncommon in SW Sweden. However, they do *not* fit the description of a further, as yet not generally accepted species, *C. repentina* Hudec (1960).

In the material, presented in tables 3 and 4, only sample No. 5 (Stubberget on Mt Kullaberg, Skåne) contains doubtful specimens, besides typical *lubrica* and *lubricella*. Provisionally, they have been referred arbitrarily to either species.

In addition, very young specimens of *Cochlicopa*, as well as of some species of *Vertigo*, *Vallonia* and clausiliids cannot always be determined accurately. When such specimens occur in samples they have been grouped in proportion to the numbers of undisputable specimens present.

Davies (1979) has recently demonstrated that the widespread *Arion hortensis* auctt. is an aggregate of 3 species. Swedish specimens prevalently, or perhaps throughout, belong to *A. distinctus* Mabille, but as long as this has not been proved extensively, I prefer to use the name *hortensis* auctt. here.

## 8. GEOGRAPHICALLY RESTRICTED SPECIES

The stock of species from which the talus and boulder slope fauna is recruited is largely the same for the whole area. There is, indeed, considerable variation in frequency and gaps in



distribution, but these can largely be attributed to local ecological differences.

Some species are, however, more or less on the border of their distribution, and for this reason absent in a large part of the area (cf. maps in Kerney and Cameron, 1979). The following species have a northern and/or inland distribution:

*Columella edentula*  
*Vertigo ronnebyensis*

*Zoogenetes harpa*  
*Discus ruderatus*

For another group of species the distribution has a southern and/or coastal character:

*Succinea oblonga*  
*Truncatellina costulata*  
*Vertigo angustior*  
*Lauria cylindracea*

*Arion intermedius*  
*Clausilia pumila*  
*Perforatella incarnata*

Finally, there is the rather enigmatic *Clausilia dubia* which cannot properly be referred to any of these groups, but may be classified tentatively as northern and inland. Apart from *T. costulata*, it is the rarest species of the area, known only from 3 sites, of which only one record is of recent origin.

## 9. SNAILS AND SLUGS

In the following account snails and slugs will be treated separately. In some respects they represent different ecological groups. Snails are protected against desiccation by their shells, whereas slugs depend entirely upon their ability to move to sheltered places with constant high relative humidity. In general, slugs move more freely in the habitat, whereas most testaceous species are relatively sedentary, particularly the minute species.

The population dynamics of slugs in a locality are in many cases probably a history of repeated local extinction during dry years, and rapid recolonization during wet years or even seasons. When present, their appearance is to a high degree a matter of weather conditions.

Therefore it is more or less a matter of chance to what extent the slug fauna of a locality can be unveiled at a particular visit. Snails, on the other hand, can be detected readily when using appropriate methods. They can long remain on seemingly dry ground, or in dry litter, and even when not present alive their occurrence may be indicated by empty shells. This makes it possible also to note the presence of seasonal species, such as *Vitrina pellucida*, at times when no living specimens can be found.

For these reasons snails and slugs must be treated separately in the present context. Using proper collecting methods, lists of snail species can be produced which have a considerable degree of significance, whereas lists of slug species are in most cases fairly incomplete.<sup>1</sup>

On the other hand slugs are, as far as their spatial presence in the habitat is concerned, much less restricted than the snails. They may fit fairly different ecological niches, but they move freely and can occur virtually together and, as far as the gross habitat is concerned, they show fairly little specialization.

Little work has been done on the pedochemical dependence of slugs, but empirical evidence suggests that they have wide ranges. None can be classified as calciphile. As far as the relation to pH is concerned, threshold values for slugs in SW Sweden, under ecological conditions relevant in the present connection, are given below.

<sup>1</sup> Methods for estimating slug populations indeed exist, e.g. by waterlogging soil samples (South, 1964), but they are only feasible under very particular conditions, and not in the present connection.



TABLE 2

Threshold pH values for slugs in SW Sweden

| pH   | Species                                                                                                                                                         |
|------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------|
| >4.0 | <i>Arion subfuscus</i> (Drap.)                                                                                                                                  |
| 4.5  | <i>Arion ater</i> (L.)<br><i>Arion silvaticus</i> Lohm.<br>* <i>Arion intermedius</i> Normand<br><i>Limax cinereoniger</i> Wolf<br><i>Limax tenellus</i> Müller |
| <5.0 | * <i>Arion fasciatus</i> (Nilsson)<br><i>Limax marginatus</i> Müller<br>* <i>Deroceras laeve</i> (Müller)                                                       |
| 5.0  | * <i>Arion circumscriptus</i> Johnston<br>* <i>Deroceras agreste</i> (L.)<br>* <i>Deroceras reticulatum</i> (Müller)                                            |
| >5.0 | * <i>Arion hortensis</i> auctt.                                                                                                                                 |

\* see text for explanation

Comments on table 2. A single record of *Limax maximus* L. from a boulder slope (at pH 6.5) is scarcely significant.

Species marked with an asterisk are either not typical for talus and boulder slope habitats or occur only in part of the area. For the rest, however, it can be postulated that in such habitats:

5 species may usually be present at pH 4.5;

6 species at pH 5.0;

further slug species are not uncommon at slightly higher pH, but so far these are more or less alien in the habitat.

There is no indication in the present material that high pH is a limiting factor for slugs, though the evidence is weak owing to scantiness of data. Actual maximum figures for slug species in different woodland habitats are given in Table 1, based on material from the province of Halland.

10. THE PROBABLE UPPER LIMIT OF CO-EXISTING SPECIES IN HABITATS

With the proviso that not all species occur over the whole area, about 45 testaceous and some 10 slug species are available for recruitment to the talus and boulder slope fauna in the ecologically optimal parts of the area; in unfavourable (i.e. oligotrophic) parts considerably less. To some extent the two groups considered in section 8, northern/inland and southern/coastal respectively, balance each other. In the following account snails only will be considered.

Depending on sample size (cf. discussion in section 4), weather conditions, population dynamics etc., all the species of a site would only rarely be expected in a sample. Extended sampling will allow an estimate, or in the best case yield the total number of species. But in a geographically extensive survey, such as the present, this is not feasible. However, an attempt will be made to estimate how many testaceous species would be expected at different pH levels, in ideal circumstances, on the basis of observations on the autecology of the individual species. From available records an estimate is made of which further species could be expected, given the following presumptions:

- (a) that they occur regularly in the same tract;
- (b) that they live under ecologically almost identical conditions.



The most oligotrophy-tolerant species are *Columella aspera*, *Nesovitrea hammonis* and *Euconulus fulvus*, not only in the area concerned here but also, it seems, generally in NW Europe (cf. Bishop, 1976; Wäreborn, 1969). They have been found already at pH 4 (though in woodland of another type, as this low pH was not measured in any of the talus or boulder slope sites of the present survey). From this base level species are added at the pH at which they turn up in the present material, provided their other ecological demands are met. Species such as *Vertigo alpestris*, *Spermodea lamellata*, *Balea perversa* and *Cepaea hortensis* are not uncommon in boulder slope habitats already at pH 5, but scarcely together in the same site.

Information on the autecology of the species within the area, of importance when estimating the potential number of species in habitats, can be obtained from Lohmander (1923), Sundler (1923) and Waldén (1969).

Considering the conditions of geographical and ecological co-existence the curve (a-a) of Figs. 3 and 4 has been tentatively constructed, representing the maximum number of testaceous species expected at different pH levels. The curves have been constructed independently on records from the southern (Fig. 3) and the northern slope sector (Fig. 4) respectively. The evidence will be discussed in section 11, concerning relation between pH and number of species. Only some comments on the significance of the 'border curve' (a-a) will be made here.

From a base level of 3 species at pH 4 there is first a rapid increase. At or beyond pH 7 the curve tends to flatten out. The highest estimates are 37 snail species at pH 7.5 in the southern slope sector, 32 species at pH 7.0 in the northern sector. If we neglect the fact that pH records above 7.5 are not available in the present material it could be questioned if any further increase of the number of species might be expected. In fact, rather the contrary seems probable.

Some species, such as *Columella aspera* and *Nesovitrea hammonis*, have their optimum in the acid range, and occur in low relative abundance or may even be absent at high pH (cf. examples in tables 3 and 4). In fact, it is doubtful if *C. aspera* can persist at high pH. When present in samples from such habitats it may have been confined to small, local spots with low pH. This, however, is a matter of microhabitats and niche specialization, which is considered only briefly in the present paper.

In this context it should be remembered that with few exceptions the samples on which the present study is based emanate from localities which are effectively non-calcareous. No species is confined to the few calcareous sites.

The hypothetical curve (a-a) may be representative for the southern sector, but is probably not valid for the whole northern sector. Some species—considered in the following section—avoid the strictly north-facing slopes, though they occur in less extremely north-facing slopes. For this reason the highest numbers of species could scarcely be expected in sites with a pronounced northern aspect.

## 11. DIVERSITY IN RELATION TO pH AND SLOPE ASPECT

With some simplification it can be stated that three gross factors control the ecological distribution of molluscs in the present material:

- (a) The calcium and trophic-factor complex, for which pH has been used as a parameter.
- (b) Topography, characterized by the criteria on talus and boulder slopes described in section 6. Even if there is a good deal of variation in microhabitat diversity it can, as a gross factor, be considered constant in the present material.
- (c) The thermoclimatic factor complex, for which no measurements are available, but which is linked to the aspect of the slope.

Under the regime of these factors, variation in shelter and moisture—*per se* of decisive importance for molluscs—play a subordinate role. The composite nature of these gross factors, and interactions between them, are beyond the scope of the present study.





Fig. 1. The area surveyed, with the localities in tables 3 and 4 indicated.

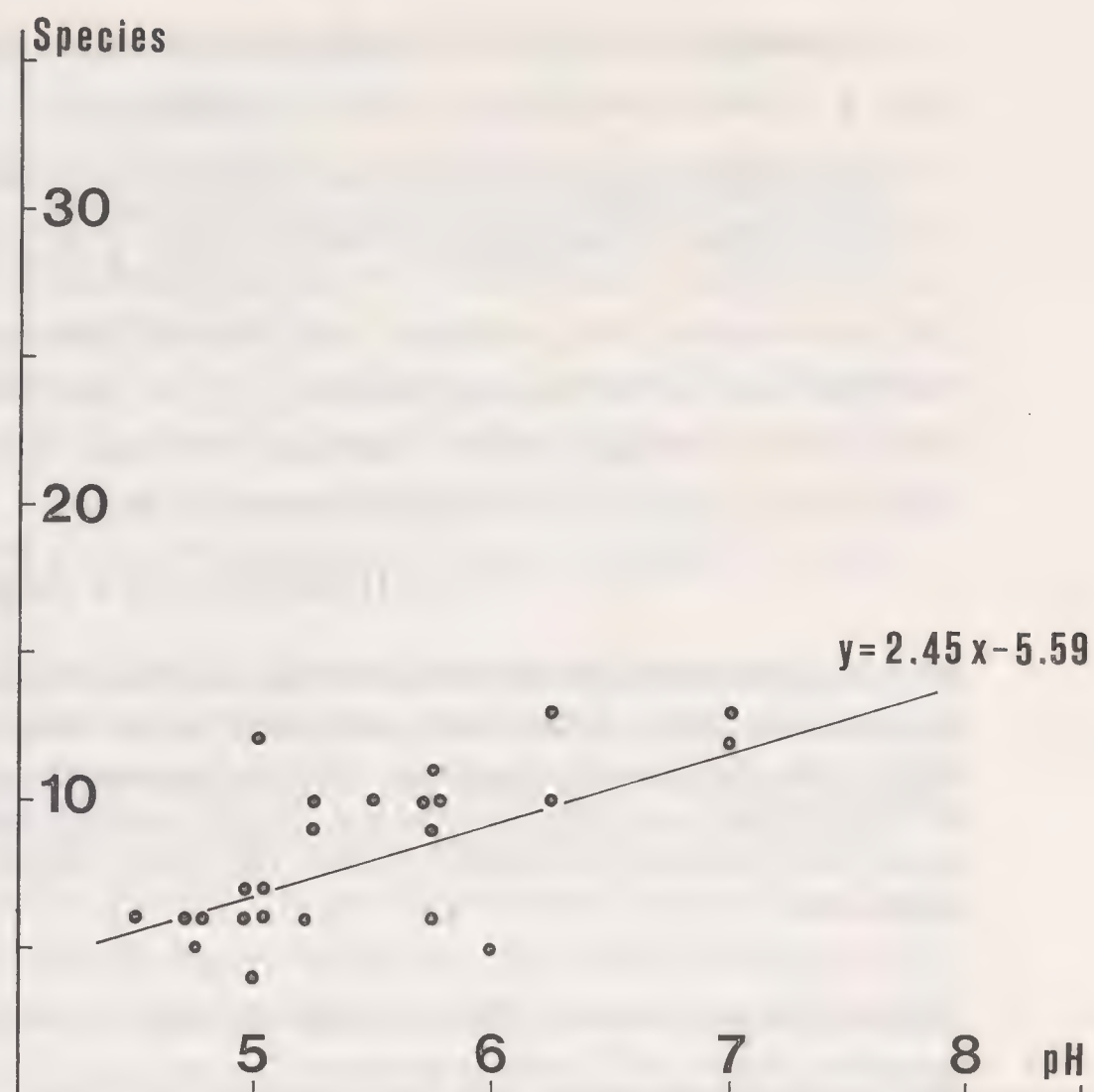


Fig. 2. Correlation between pH and number of testaceous species in woodland on flat ground.

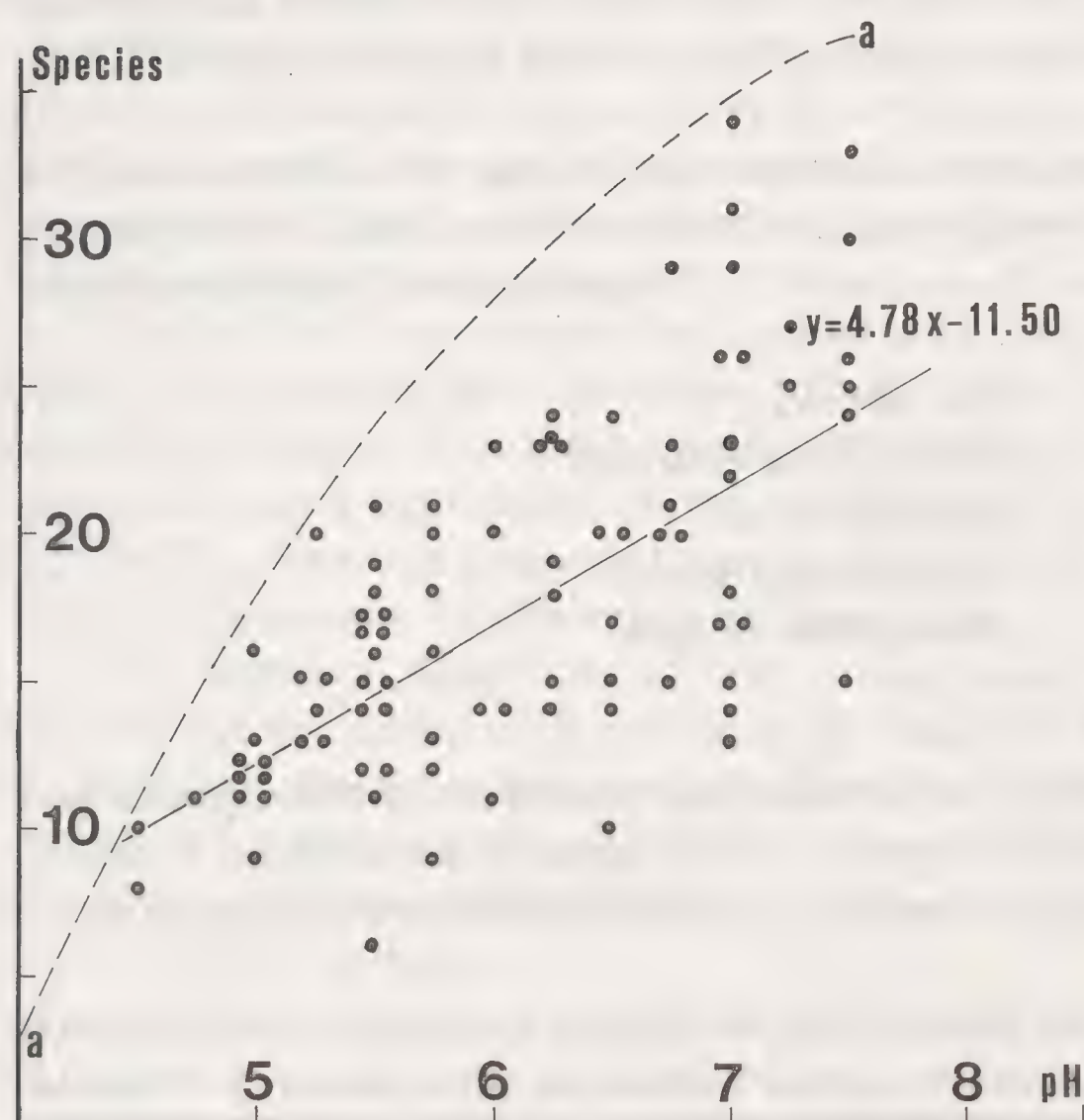


Fig. 3. Correlation between pH and number of testaceous species in wooded taluses and boulder slopes in the southern slope sector.

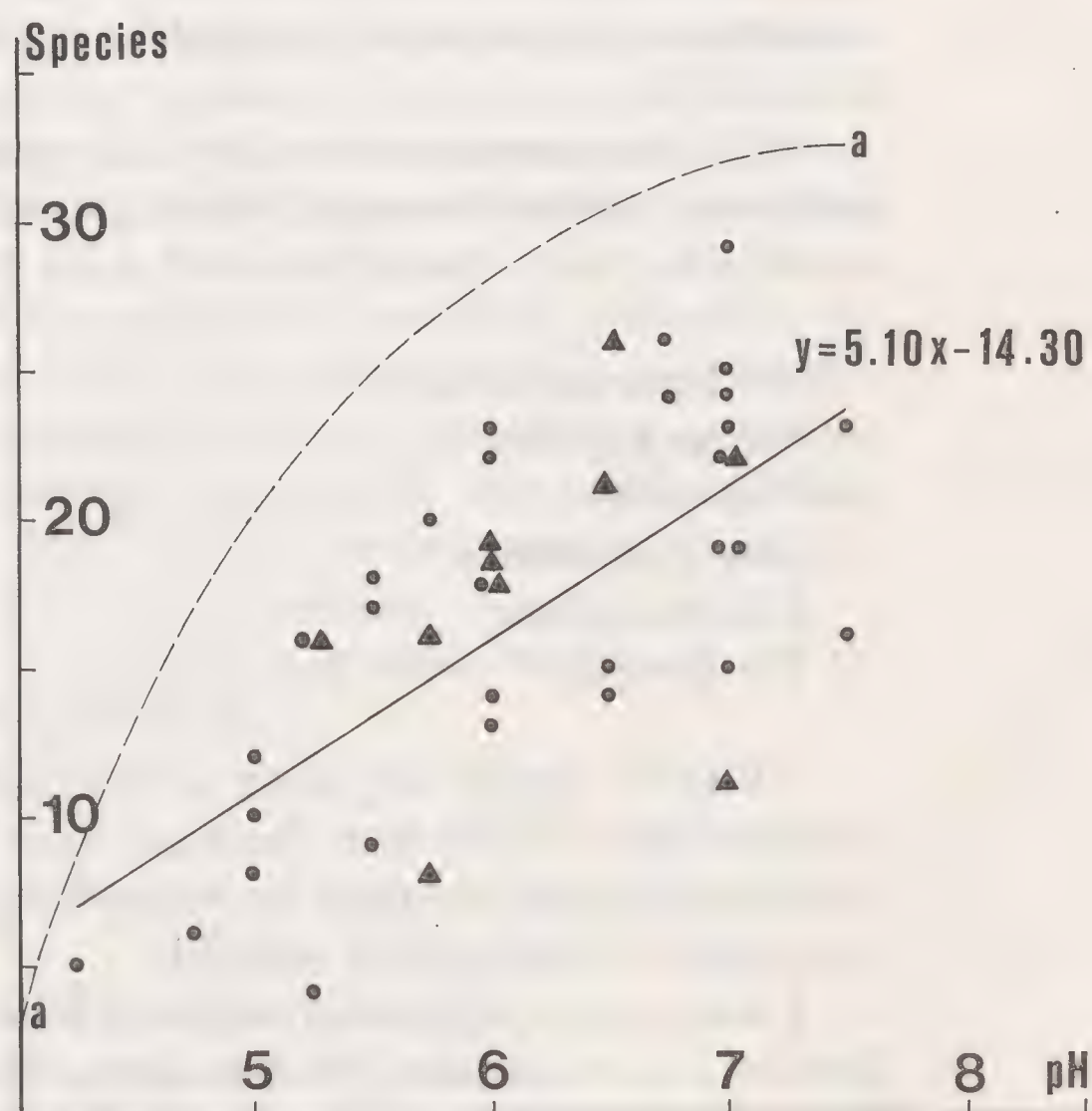


Fig. 4. Correlation between pH and number of testaceous species in wooded taluses and boulder slopes in the northern slope sector. Triangles: strictly north-facing sites.

Curve (a-a) represents the maximum number of species which might be expected at different pH levels (further explanation on p 360).



*Correlation with pH.* The clear and basic character of this correlation is evident from Figs. 3 and 4. The correlation is very strong:

Southern slope sector:  $r = 0.6614$ ;  $p < 0.001$

Northern slope sector:  $r = 0.6758$ ;  $p < 0.001$

In both cases the average number of species increases by about 5 species per pH unit. A comparison between regressions for the southern and northern slope sectors record, based on  $t$ -analysis according to the classical method (Bonnier and Tedin, 1962, p. 158), shows that they agree well, even if the significance is weak:

$$t = 0.3029 \text{ at } 124 \text{ degrees of freedom; } p < 0.8$$

*Note on application of pH data in diagrams.* In cases where there is a difference between the 2 or more pH values obtained from each sample (cf. section 3), only the highest value has been used in the construction of the diagrams, and the calculation of regression equations. This is because within the pertinent range of pH (4.0–7.5) it is nearly always a lower pH limit which can come in question. The highest pH obtained from a site indicates which species may potentially be there, and referring the total number of species in the sample to the highest pH value is consequently the best alternative.

*Aspect of slope.* As considered above and demonstrated by the diagrams, the average numbers of species at any pH level is almost the same in the southern and northern slope sectors. If attention is concentrated on the small fraction (10 samples) from strictly north-facing sites, marked by triangles in Fig. 4, even these do not differ noticeably from the rest of the material. However, the number is too small for statistically significant evidence ( $t = 0.844$ ;  $p > 0.4$ ).

But even if there is more or less the same number of species, irrespective of the aspect of the slope, there is a clear difference in maximum diversity. In the northern slope sector the highest number of snail species found co-existing in one site is 29 (Table 4, No. 15), whereas this number is reached or exceeded in 6 sites of the south sector, the highest number being 34 species (Table 3, No. 10).

With the reservation that for some species the records are so few that their absence may be incidental rather than significant, the following species have not been found in the strictly north-facing sites, though most of them have been found in less pronounced northern slopes:

*Truncatellina costulata*

*Vertigo pygmaea*

*V. angustior*

*Lauria cylindracea*

*Vallonia costata*

*V. excentrica*

*Ena obscura*

*Macrogastra ventricosa*

*Balea perversa*

*Bradybaena fruticum*

*Euomphalia strigella*

All these species are more or less southern in distribution, and most of them prefer well insulated sites. To be sure, there are some further species which have not been found in strictly north-facing sites, but these are synanthropic or otherwise alien in the habitats and therefore not significant in the present context.

Furthermore, *Zoogenetes harpa* and *Clausilia dubia*, which both have a northern distribution in Sweden, have not been found in sites in the northern sector within the surveyed area. Probably this is accidental, depending on their extreme rarity, though it cannot be excluded that they have particular ecological demands which cannot be satisfied in marginal localities outside their main area. In every case they are not uncommon in north-facing sites in their more northern main area.

The species which are lacking in the strictly north-facing sites, or are generally disfavoured in the northern slope sector, are all more or less 'on the top' of the communities, and come in first when there is a relatively complete representation of the more eurytopic species. This explains



why maximum numbers of species could not be expected to be as high in north-facing sites as in south-facing sites, even if the average diversity is the same.

But even if the main pattern of diversity is largely the same, irrespective of the aspect of the slope, there are, indeed, considerable differences with regard to frequency and abundance of the individual species related to the differences in bioclimate in slopes of different aspect. This, however, is a theme which falls beyond the present study.

## 12. EXAMPLES OF MOLLUSC COMMUNITIES IN TALUS AND BOULDER SLOPES

The examples given in tables 3 and 4, drawn from sites in the southern and northern sectors of slope aspect respectively, are intended to demonstrate (a) how the array of species can vary at different levels of diversity, (b) the most pronounced high diversity communities. Consequently, examples are chosen in order to demonstrate variance rather than consistency in trends.

More extensive material is presented from sites in the southern slope sector, partly because the material available is larger and allows a more varied representation, and partly because the display of stenotopic, or otherwise interesting species, is greater here and if to be more examples well documented.

All figures are based only on specimens collected alive. In all 17,815 specimens of snails were collected and examined from the 15 sites considered here, of which 14,052 were collected alive. For slugs, the data are largely based on field records.

For snails the following symbols have been used:

+ indicates that only empty shells have been found, or that the species has been observed in the locality, but is not present in the sample.

\* indicates that the figure for the species is somewhat enhanced because the numbers of specimens obtained by direct collecting, or by sweeping the vegetation, have been added to the number present in the quantitative sample. In most cases the figures are increased only slightly for this reason. Only for *Columella aspera* in localities 1 and 3 has this led to substantially modified figures and dominance values.

The fact that for some species a substantial part of the population may not be present in the litter, but climbing the vegetation, hiding under the bark of logs etc., makes a quantitative sampling of the entire mollusc community extremely complicated. Except for the few, apparent cases of *C. aspera* considered above, the adding of specimens obtained by other methods than litter sifting does not necessarily imply that the species is over-represented compared with its relative abundance in the entire mollusc community of a gross habitat.

The statistical treatment of very young specimens of certain genera, which cannot be determined to species with certainty, is considered in section 7.

For slugs the following symbols have been used:

- + 1 specimen found
- + + 2–9 specimens found
- + + + 10 or more

### *Description of the localities*

Concerning the vegetation, the following plants are both well known to everyone (though in some cases different species may be prevalent in Sweden than e.g. in England) and commonly present in the boulder slope habitats, and their Latin names will not be repeated in the descriptions:

Linden (*Tilia cordata* Mill.), Maple (*Acer platanoides* L.), Rowan (*Sorbus aucuparia* L.), Elm



TABLE 3 Land mollusc communities in talus and

| Locality No.                          | 1.     |        | 2.  |        | 3.  |        | 4.      |        |
|---------------------------------------|--------|--------|-----|--------|-----|--------|---------|--------|
| pH                                    | >5-5.5 |        | 4.5 |        | 5.5 |        | 7.0-7.5 |        |
| Slope direction                       | E      |        | E   |        | WSW |        | S       |        |
| Number of species:                    |        |        |     |        |     |        |         |        |
| I. Snails                             | 6      |        | 8   |        | 11  |        | 15      |        |
| II. Slugs                             | 1      |        | —   |        | 4   |        | 2       |        |
| Living specimens N                    | N      |        | N   |        | N   |        | N       |        |
| Dominance D                           | D%     |        | D%  |        | D%  |        | D%      |        |
| I. Snails                             |        |        |     |        |     |        |         |        |
| <i>Carychium tridentatum</i> (Risso)  | —      | —      | —   | —      | 5   | 1.45   | —       | —      |
| <i>Succinea putris</i> (L.)           | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Cochlicopa lubrica</i> (Müll.)     | 92     | 19.25  | —   | —      | —   | —      | —       | —      |
| <i>Cochlicopa lubricella</i> (Porro)  | —      | —      | —   | —      | —   | —      | 14      | 2.58   |
| <i>Columella edentula</i> (Drap.)     | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Columella aspera</i> Waldén        | 101*   | 21.13* | 6   | 9.38   | 69* | 19.90* | 14*     | 2.58*  |
| <i>Vertigo pusilla</i> Müll.          | —      | —      | —   | —      | —   | —      | 133     | 24.49  |
| <i>Vertigo substriata</i> (Jeffr.)    | 146    | 30.54  | 17  | 26.56  | 14  | 4.05   | 59      | 10.87  |
| <i>Vertigo pygmaea</i> (Drap.)        | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Vertigo ronnebyensis</i> (Wstld)   | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Vertigo alpestris</i> Alder        | —      | —      | 11  | 17.19  | 3   | 0.87   | 55      | 10.13  |
| <i>Vertigo angustior</i> Jeffr.       | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Lauria cylindracea</i> (da Costa)  | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Vallonia costata</i> (Müll.)       | —      | —      | —   | —      | —   | —      | 64      | 11.79  |
| <i>Acanthinula aculeata</i> (Müll.)   | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Zoogenetes harpa</i> (Say)         | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Ena obscura</i> (Müll.)            | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Punctum pygmaeum</i> (Drap.)       | —      | —      | —   | —      | 39  | 11.27  | 68      | 12.52  |
| <i>Discus ruderatus</i> (Fér.)        | —      | —      | 5   | 7.81   | —   | —      | —       | —      |
| <i>Discus rotundatus</i> (Müll.)      | 52     | 10.88  | 6   | 9.38   | 112 | 32.37  | 39      | 7.18   |
| <i>Vitrina pellucida</i> (Müll.)      | —      | —      | —   | —      | —   | —      | 15      | 2.76   |
| <i>Vitrea crystallina</i> (Müll.)     | —      | —      | —   | —      | 5   | 1.45   | —       | —      |
| <i>Vitrea contracta</i> (Wstld)       | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Nesovitrea hammonis</i> (Ström)    | 47     | 9.83   | 7   | 10.94  | 17  | 4.91   | 7       | 1.29   |
| <i>Nesovitrea petronella</i> (Pfr)    | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Aegopinella pura</i> (Alder)       | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Aegopinella nitidula</i> (Drap.)   | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Oxychilus cellarius</i> (Müll.)    | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Oxychilus alliarius</i> (Miller)   | —      | —      | 4   | 6.25   | 1   | 0.29   | 7       | 1.29   |
| <i>Euconulus fulvus</i> (Müll.)       | 40     | 8.37   | 8   | 12.50  | 81  | 23.41  | 36      | 6.63   |
| <i>Cochlodina laminata</i> (Mont.)    | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Macrogastra ventricosa</i> (Drap.) | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Macrogastra plicatula</i> (Drap.)  | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Clausilia bidentata</i> (Ström)    | —      | —      | —   | —      | —   | —      | 31      | 5.71   |
| <i>Clausilia pumila</i> Pfr           | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Balea perversa</i> (L.)            | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Bradybaena fruticum</i> (Müll.)    | —      | —      | —   | —      | —   | —      | 1       | 0.18   |
| <i>Trichia hispida</i> (L.)           | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Euomphalia strigella</i> (Drap.)   | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Arianta arbustorum</i> (L.)        | —      | —      | —   | —      | —   | —      | —       | —      |
| <i>Helicigona lapicida</i> (L.)       | —      | —      | —   | —      | —   | —      | +       | +      |
| <i>Cepaea hortensis</i> (Müll.)       | —      | —      | —   | —      | +   | +      | —       | —      |
| Snails, total                         | 478    | 100.00 | 64  | 100.01 | 346 | 100.01 | 543     | 100.00 |
| II. Slugs                             |        |        |     |        |     |        |         |        |
| <i>Arion ater</i> (L.)                | +      |        | —   |        | ++  |        | ++      |        |
| <i>Arion subfuscus</i> (Drap.)        | —      |        | —   |        | +   |        | —       |        |
| <i>Arion fasciatus</i> (Nilsson)      | —      |        | —   |        | —   |        | —       |        |
| <i>Arion silvaticus</i> Lohmander     | —      |        | —   |        | —   |        | —       |        |
| <i>Arion intermedius</i> Normand      | —      |        | —   |        | —   |        | —       |        |
| <i>Limax cinereoniger</i> Wolf        | —      |        | —   |        | +   |        | —       |        |
| <i>Limax tenellus</i> Müll.           | —      |        | —   |        | +   |        | —       |        |
| <i>Limax marginatus</i> Müll.         | —      |        | —   |        | —   |        | +       |        |
| <i>Deroceras reticulatum</i> (Müll.)  | —      |        | —   |        | —   |        | —       |        |



boulder slope habitats, in the southern slope sector

| 5.<br>6.0->6<br>S |       | 6.<br>6.0<br>SW |       | 7.<br><7<br>SE |        | 8.<br>7.5<br>WSW |        | 9.<br>7.0-7.5<br>ESE |       | 10.<br>7.0<br>SW |        |
|-------------------|-------|-----------------|-------|----------------|--------|------------------|--------|----------------------|-------|------------------|--------|
| 18<br>1           |       | 20<br>2         |       | 23<br>5        |        | 31<br>6          |        | 33<br>5              |       | 34<br>5          |        |
| N                 | D%    | N               | D%    | N              | D%     | N                | D%     | N                    | D%    | N                | D%     |
| 56                | 2.58  | 35              | 6.39  | 162            | 34.54  | 341              | 31.93  | 75                   | 4.21  | 91               | 4.14   |
| —                 | —     | —               | —     | —              | —      | —                | —      | —                    | —     | 3                | 0.14   |
| 163               | 7.52  | 11              | 2.01  | 32             | 6.82   | 37               | 3.46   | 86                   | 4.82  | 110              | 5.00   |
| 26                | 1.20  | 1               | 0.18  | —              | —      | 147              | 13.76  | 29                   | 1.63  | 4                | 0.18   |
| —                 | —     | —               | —     | —              | —      | 29               | 2.72   | 11                   | 0.62  | 14               | 0.64   |
| 54                | 2.49  | 2               | 0.36  | 4              | 0.85   | 25               | 2.34   | 1                    | 0.06  | 2                | 0.09   |
| 280               | 12.92 | 3               | 0.55  | 8              | 1.71   | 24               | 2.25   | 89                   | 4.99  | 83               | 3.78   |
| 660               | 30.45 | 50              | 9.12  | 16             | 3.41   | 24               | 2.25   | 76                   | 4.26  | 94               | 4.28   |
| —                 | —     | —               | —     | —              | —      | —                | —      | +                    | +     | —                | —      |
| —                 | —     | 4               | 0.73  | 6              | 1.28   | —                | —      | 3                    | 0.17  | 27               | 1.23   |
| —                 | —     | 3               | 0.55  | 6              | 1.28   | 2                | 0.19   | 22                   | 1.23  | 62               | 2.82   |
| —                 | —     | —               | —     | —              | —      | —                | —      | 637                  | 35.72 | 33               | 1.50   |
| 71                | 3.28  | —               | —     | —              | —      | —                | —      | —                    | —     | —                | —      |
| —                 | —     | —               | —     | —              | —      | 1                | 0.09   | 194                  | 10.88 | 41               | 1.87   |
| 59                | 2.72  | 1               | 0.18  | —              | —      | 17               | 1.59   | 18                   | 1.01  | 7                | 0.32   |
| —                 | —     | —               | —     | —              | —      | +                | +      | —                    | —     | —                | —      |
| —                 | —     | —               | —     | —              | —      | +                | +      | —                    | —     | 1                | 0.05   |
| 107               | 4.94  | 76              | 13.87 | 21             | 4.48   | 248              | 23.22  | 160                  | 8.97  | 910              | 41.41  |
| —                 | —     | —               | —     | 26             | 5.54   | —                | —      | 10                   | 0.56  | 49               | 2.22   |
| 269               | 12.41 | 235             | 42.88 | 42             | 8.95   | 10               | 0.94   | 17                   | 0.95  | 127              | 5.78   |
| —                 | —     | —               | —     | +              | +      | 1                | 0.09   | 10                   | 0.56  | 1                | 0.05   |
| —                 | —     | 42              | 7.66  | —              | —      | —                | —      | 40                   | 2.24  | 18               | 0.82   |
| 11                | 0.51  | —               | —     | 2              | 0.43   | +                | +      | —                    | —     | —                | —      |
| 202               | 9.32  | 20              | 3.65  | 49             | 10.45  | 18               | 1.69   | 23                   | 1.29  | 111              | 5.05   |
| —                 | —     | 8               | 1.46  | 19             | 4.05   | 2                | 0.19   | 13                   | 0.73  | 12               | 0.55   |
| —                 | —     | 4               | 0.73  | 7              | 1.49   | 27               | 2.53   | 6                    | 0.34  | 24               | 1.09   |
| 2                 | 0.09  | —               | —     | —              | —      | 6                | 0.56   | —                    | —     | 23               | 1.05   |
| —                 | —     | —               | —     | —              | —      | 1                | 0.09   | +                    | +     | +                | +      |
| 3                 | 0.14  | —               | —     | 2              | 0.43   | —                | —      | 2                    | 0.11  | 1                | 0.05   |
| 195               | 9.00  | 41              | 7.48  | 46             | 9.81   | 40               | 3.75   | 73                   | 4.09  | 199              | 9.06   |
| —                 | —     | 2               | 0.36  | 8              | 1.71   | 17               | 1.59   | 31                   | 1.74  | 19               | 0.86   |
| —                 | —     | —               | —     | —              | —      | 8                | 0.75   | —                    | —     | —                | —      |
| —                 | —     | —               | —     | 1              | 0.18   | —                | —      | 27                   | 2.53  | 81               | 3.69   |
| 7                 | 0.32  | 9               | 1.64  | 1              | 0.21   | 9                | 0.84   | 8                    | 0.45  | 23               | 1.05   |
| —                 | —     | —               | —     | 8              | 1.71   | —                | —      | —                    | —     | —                | —      |
| 1                 | 0.05  | —               | —     | —              | —      | —                | —      | 6                    | 0.34  | —                | —      |
| —                 | —     | —               | —     | 1              | 0.21   | 3                | 0.28   | —                    | —     | +                | +      |
| —                 | —     | —               | —     | —              | —      | —                | —      | 5                    | 0.28  | 6                | 0.27   |
| —                 | —     | —               | —     | —              | —      | +                | +      | 7                    | 0.39  | —                | —      |
| —                 | —     | —               | —     | —              | —      | 1                | 0.09   | 13                   | 0.73  | 7                | 0.32   |
| 1                 | 0.05  | +               | +     | 1              | 0.21   | 2                | 0.19   | 13                   | 0.73  | 11               | 0.50   |
| —                 | —     | —               | —     | 2              | 0.43   | 1                | 0.09   | 1                    | 0.06  | 3                | 0.14   |
| 2167              | 99.99 | 548             | 99.98 | 469            | 100.00 | 1068             | 100.00 | 1783                 | 99.99 | 2197             | 100.00 |

|   |    |     |    |    |    |
|---|----|-----|----|----|----|
| — | ++ | +++ | ++ | +  | —  |
| — | —  | ++  | +  | ++ | +  |
| — | —  | —   | ++ | —  | —  |
| — | —  | +   | +  | +  | ++ |
| + | —  | —   | —  | —  | —  |
| — | —  | ++  | +  | —  | +  |
| — | +  | —   | ++ | +  | +  |
| — | —  | ++  | —  | +  | —  |
| — | —  | —   | —  | —  | ++ |



TABLE 4

Land mollusc communities in talus and boulder slope habitats, in the northern slope sector

|                                       |     |        |         |       |         |        |         |        |     |        |
|---------------------------------------|-----|--------|---------|-------|---------|--------|---------|--------|-----|--------|
| Locality No.                          | 11. |        | 12.     |       | 13.     |        | 14.     |        | 15. |        |
| pH                                    | 5.0 |        | 5.0-5.0 |       | 6.0-7.0 |        | 6.0-6.5 |        | 7.0 |        |
| Slope direction                       | NW  |        | NE      |       | N       |        | N       |        | NE  |        |
| Number of species:                    |     |        |         |       |         |        |         |        |     |        |
| I. Snails                             | 6   |        | 16      |       | 22      |        | 26      |        | 29  |        |
| II. Slugs                             | —   |        | 1       |       | 5       |        | 4       |        | 4   |        |
| Living specimens N                    | N   |        | N       |       | N       |        | N       |        | N   |        |
| Dominance D                           | D%  |        | D%      |       | D%      |        | D%      |        | D%  |        |
| I. Snails                             |     |        |         |       |         |        |         |        |     |        |
| <i>Carychium tridentatum</i>          | —   | —      | 234     | 16.88 | 141     | 20.52  | 400     | 29.28  | 210 | 22.83  |
| <i>Cochlicopa lubrica</i>             | —   | —      | 43      | 3.10  | 37      | 5.39   | 49      | 3.59   | 29  | 3.15   |
| <i>Cochlicopa lubricella</i>          | —   | —      | —       | —     | —       | —      | 1       | 0.07   | 10  | 1.09   |
| <i>Columella edentula</i>             | —   | —      | —       | —     | 18      | 2.62   | 21*     | 1.54*  | 62  | 6.74   |
| <i>Columella aspera</i>               | 1   | 3.33   | 44      | 3.17  | —       | —      | 16*     | 1.17*  | —   | —      |
| <i>Vertigo pusilla</i>                | —   | —      | 21      | 1.52  | 11      | 1.60   | 8       | 0.59   | 6   | 0.65   |
| <i>Vertigo substriata</i>             | 8   | 26.67  | 178     | 12.84 | 38      | 5.53   | 240     | 17.57  | 15  | 1.63   |
| <i>Vertigo ronnebyensis</i>           | 4   | 13.33  | —       | —     | 5       | 0.73   | —       | —      | —   | —      |
| <i>Vertigo alpestris</i>              | 2   | 6.67   | —       | —     | 4       | 0.58   | —       | —      | +   | +      |
| <i>Vallonia costata</i>               | —   | —      | —       | —     | —       | —      | —       | —      | 1   | 0.11   |
| <i>Acanthinula aculeata</i>           | —   | —      | —       | —     | —       | —      | 126     | 9.22   | 39  | 4.24   |
| <i>Spermodea lamellata</i> (Jeffr.)   | —   | —      | —       | —     | —       | —      | 16      | 1.17   | —   | —      |
| <i>Ena obscura</i>                    | —   | —      | —       | —     | —       | —      | —       | —      | +   | +      |
| <i>Punctum pygmaeum</i>               | —   | —      | 398     | 28.72 | 218     | 31.73  | 164     | 12.01  | 324 | 35.22  |
| <i>Discus ruderatus</i>               | —   | —      | —       | —     | 5       | 0.73   | 6       | 0.44   | 2   | 0.22   |
| <i>Discus rotundatus</i>              | —   | —      | 277     | 19.99 | 77      | 11.21  | 68      | 4.98   | 17  | 1.85   |
| <i>Vitrina pellucida</i>              | —   | —      | —       | —     | —       | —      | 3       | 0.22   | 6   | 0.65   |
| <i>Vitrea crystallina</i>             | —   | —      | 7       | 0.51  | 16      | 2.33   | 36      | 2.64   | 26  | 2.83   |
| <i>Vitrea contracta</i>               | —   | —      | 2       | 0.14  | —       | —      | —       | —      | 6   | 0.65   |
| <i>Nesovitrea hammonis</i>            | 3   | 10.00  | 41      | 2.96  | 19      | 2.77   | 40      | 2.93   | 28  | 3.04   |
| <i>Nesovitrea petronella</i>          | —   | —      | —       | —     | 7       | 1.02   | 16      | 1.17   | —   | —      |
| <i>Aegopinella pura</i>               | —   | —      | 1       | 0.07  | 2       | 0.29   | 10      | 0.73   | 26  | 2.83   |
| <i>Aegopinella nitidula</i>           | —   | —      | —       | —     | —       | —      | 12      | 0.88   | 1   | 0.11   |
| <i>Oxychilus cellarius</i>            | —   | —      | —       | —     | +       | +      | —       | —      | +   | +      |
| <i>Oxychilus alliarius</i>            | —   | —      | 25      | 1.80  | 3       | 0.44   | +       | +      | +   | +      |
| <i>Euconulus fulvus</i>               | 12  | 40.00  | 104     | 7.50  | 53      | 7.71   | 99      | 7.25   | 74  | 8.04   |
| <i>Cochlodina laminata</i>            | —   | —      | —       | —     | 8       | 1.16   | 1       | 0.07   | 3   | 0.33   |
| <i>Macrogastra ventricosa</i>         | —   | —      | —       | —     | —       | —      | —       | —      | 8   | 0.87   |
| <i>Macrogastra plicatula</i>          | —   | —      | —       | —     | 9       | 1.31   | 3       | 0.22   | 17* | 1.85*  |
| <i>Clausilia bidentata</i>            | —   | —      | 8       | 0.58  | 11      | 1.60   | 4       | 0.29   | 6   | 0.65   |
| <i>Clausilia pumila</i>               | —   | —      | 2       | 0.14  | —       | —      | 26      | 1.90   | —   | —      |
| <i>Perforatella incarnata</i> (Müll.) | —   | —      | —       | —     | —       | —      | 1       | 0.07   | —   | —      |
| <i>Trichia hispida</i>                | —   | —      | —       | —     | 1       | 0.15   | —       | —      | —   | —      |
| <i>Arianta arbustorum</i>             | —   | —      | 1       | 0.07  | 4       | 0.58   | +       | +      | 4   | 0.43   |
| <i>Helicigona lapicida</i>            | —   | —      | —       | —     | —       | —      | —       | —      | +   | +      |
| <i>Cepaea hortensis</i>               | —   | —      | —       | —     | —       | —      | —       | —      | +   | +      |
| Snails, total                         | 30  | 100.00 | 1386    | 99.99 | 687     | 100.00 | 1366    | 100.00 | 920 | 100.01 |
| II. Slugs                             |     |        |         |       |         |        |         |        |     |        |
| <i>Arion ater</i>                     | —   | —      | +       | —     | —       | —      | —       | —      | —   | —      |
| <i>Arion subfuscus</i>                | —   | —      | —       | —     | +       | —      | +       | —      | ++  | ++     |
| <i>Arion circumscriptus</i> Johnston  | —   | —      | —       | —     | +       | —      | —       | —      | —   | —      |
| <i>Arion silvaticus</i>               | —   | —      | —       | —     | ++      | —      | ++      | —      | ++  | ++     |
| <i>Limax cinereoniger</i>             | —   | —      | —       | —     | —       | —      | +       | —      | —   | —      |
| <i>Limax tenellus</i>                 | —   | —      | —       | —     | +       | —      | ++      | —      | +   | +      |
| <i>Limax marginatus</i>               | —   | —      | —       | —     | +       | —      | —       | —      | +   | +      |



(*Ulmus glabra* Huds.), Oak (*Quercus robur* L., in poor, stony habitats sometimes together with *Q. petraea* (Matt.) Liebl.), Beech (*Fagus silvatica* L.), Birch (*Betula verrucosa* Ehrh.), Hazel (*Corylus avellana* L.), Aspen (*Populus tremula* L.), Spruce (*Picea abies* (L.) Karst.), Pine (*Pinus silvestris* L.), Juniper (*Juniperus communis* L.), Cowberry (*Vaccinium vitis-idaea* L.), Bilberry (*V. myrtillus* L.), Raspberry (*Rubus idaeus* L.).

*I. In the southern slope sector (Table 3).*

1. Halland province, Knäred parish, between Hovshult and Körsveka, 900 m SW bench mark 149.8. Moss-covered boulder talus on the E. slope of a gneiss hill. Open stand of birch, aspen, pine and rowan, with at the top of the talus along the precipice hornbeam (*Carpinus betulus* L.). Dominating bilberry and cowberry, *Calamagrostis arundinacea* L., *Deschampsia flexuosa* (L.) Trin., ferns: *Dryopteris filix-mas* (L.) Schott, *Lastrea dryopteris* (L.) Bory, and *L. phegopteris* (L.) Bory, *Polypodium vulgare* L., raspberry, and heather (*Calluna vulgaris* (L.) Hull.), some *Chamaenerion angustifolium* (L.) Scop.—21.7.1966.

2. Västergötland province, Mjöbäck parish, Överlida, 300 m N of the SW end of Lake L. Hallängen. Moss-covered, E-facing boulder talus of gneiss, with birch-spruce wood, and some intermixture of aspen, rowan, beech and *Salix caprea* L. Raspberry, *Deschampsia flexuosa*, *Dryopteris spinulosa* (Müll.) Watt, *Trientalis europaea* L., sparse bilberry and cowberry.—19.6.1967.

3. Bohuslän province, Ucklun parish, 300 m N of St. Komperöd. Oakwood in boulder talus and stone screes to WSW, below a precipice of greyish gneiss. Some hazel, rowan. Rather sparse vegetation of *Deschampsia flexuosa*, bilberry, raspberry, *Calamagrostis arundinacea*, *Oxalis acetosella* L., *Dryopteris filix-mas* etc., only patches of mosses. At the foot of the slope dominating hazel, bilberry, *Lastrea dryopteris*, *Campanula persicifolia* L. and honeysuckle (*Lonicera periclymenum* L.).—4.8.1964.

4. Halland province, Lindberg parish, the S slope of the gneiss hill Trönningeberget. Strongly weathered and precipitous, with ledges and boulder taluses, locally very large and piled up boulders. Pine, elm, aspen, juniper, intermixture of blackthorn (*Prunus spinosa* L.), wild roses (*Rosa canina* auctt.), birch, rowan etc. Rich ground vegetation with *Calamagrostis arundinacea*, *Poa nemoralis* L., *Oxalis acetosella*, *Anemona hepatica* L., *Mercurialis perennis* L., ivy (*Hedera helix* L.), *Dryopteris filix-mas*, honeysuckle and some bilberry, on mossy boulders *Polypodium vulgare*. Partly rather xerophilous, with *Geranium sanguineum* L. and *lucidum* L., *Vicia cassubica* L., *Filipendula vulgaris* Moench and *Sedum telephium* L.—10.6.1968.

5. Skåne province (Scania), Mt Kullaberg, the S. slope of the hill Stuberget (of hornblende-gneiss). Talus with wood in the upper and lower part, of elm, oak, hawthorn (*Crataegus* sp.), some ash (*Fraxinus excelsior* L.). *Dryopteris filix-mas*, *Geranium robertianum* L., grass, below the precipice also raspberry and brambles (*Rubus* sp.), some mosses. In the middle part of the talus no trees and only sparse occurrence of herbs and ferns.—10.9.1963.

6. Bohuslän province, Hjärtum parish, Hästered, 500 m N of the crossroad. Boulder talus below a precipice of greyish gneiss to SW. Rather shady wood of oak, spruce and hazel, some aspen, bird-cherry (*Prunus padus* L.), linden and maple. Rather sparse vegetation of various grasses, raspberry, *Geranium robertianum*, *Dryopteris filix-mas*, *Oxalis acetosella*. Very rich leaf litter, only patches of mosses. At the foot of the slope, on moist ground, *Equisetum silvaticum* L. and *Athyrium filix-femina* (L.) Roth.—3.8.1964.



7. Västergötland province, Torestorp parish, 1 km NNE of Svansjö. Boulder talus and stone screes below a gneiss precipice to ESE. Oak, linden, hazel, sparse intermixture of birch, rowan, juniper and aspen. Patchy vegetation of *Dryopteris filix-mas*, *Poa nemoralis*, *Calamagrostis arundinacea*, raspberry, *Vicia sepium* L., some *Geranium robertianum* and nettles (*Urtica dioica* L.), on the boulders mosses and lichens. In the lower part very large boulders and only scattered trees; at the foot again shady with dense vegetation of *Oxalis acetosella*, *Anemone nemorosa* L. and grass.—27.5.1967.

8. Dalsland province, Tisselskog parish, Buterud, 250 m NNW bench mark 121. Hill slope to WSW, partly of calcareous slate, with boulders and stone screes. Luxuriant wood of linden, hazel, intermixed with aspen, birch, spruce, maple, yew (*Taxus baccata* L.) and fly-honeysuckle (*Lonicera xylosteum* L.). Rather sparse vegetation of *Anemone hepatica*, *Rubus saxatilis* L., *Oxalis acetosella*, *Actaea spicata* L., *Origanum vulgare* L., *Calamagrostis arundinacea*, *Melica nutans* L., *Dryopteris filix-mas*, on mossy boulders *Polypodium vulgare*. In between partly bare soil, with patches of the moss *Rhytidiadelphus triquetrus* (L.) Warnst. Below the boulder slope trivial vegetation of bilberry, cowberry, grass and *Convallaria majalis* L.—28.9.1967.

9. Västergötland province, Flo parish, Bragnum, 500 m SSE bench mark 154, the ESE slope of the Hunneberg table-mountain. High, quite vertical, precipitous dolerite cliffs above, below large dolerite taluses underlain and to some extent intermixed with strata of Palaeozoic alum shales and sandstones. At the upper margin of the talus rather dry vegetation of oak, elm, maple, hazel, linden, spruce etc., with *Geranium robertianum*, *Poa nemoralis*, *Origanum vulgare*, *Sedum rupestre* L. and *Anemone hepatica*; only patches of mosses. Below, coarse boulders mainly with mosses and lichens, and only a few trees. Further down a more gentle slope with a shady wood of ash, spruce, oak, hazel, elm, fly-honeysuckle, mainly *Oxalis acetosella*, *Geranium robertianum*, *Actaea spicata*, grass and raspberry, some nettles, *Paris quadrifolia* L. and ferns.—16.8.1963.

10. Bohuslän province, Uddevalla, Bratteröd (1700 m ESE of Gustafsberg manor house). Boulder talus and stone screes to SW, below a precipice of greyish gneiss. Luxuriant wood of oak, linden, elm, hazel, some alder (*Alnus glutinosa* (L.) Gaertn.), spruce, bird-cherry etc. Rather sparse but varying vegetation with *Poa nemoralis*, *Anemone hepatica*, *Mercurialis perennis*, *Impatiens noli-tangere* L., raspberry, *Geranium robertianum* and *Origanum vulgare*. In the lower part damp, with *Dryopteris spinulosa*, *Impatiens noli-tangere* and dense moss-carpet.—12.8.1964.

## II. In the northern slope sector.

11. Halland province, Fagered parish, 300 m S of Sågbacken, below the NW-facing steep of a gneiss hill. Old, shady sprucewood in a moss-covered boulder slope. Scattered birches, aspens and rowans. Sparse vegetation of bilberry, cowberry, *Deschampsia flexuosa*, *Dryopteris spinulosa*, *Linnaea borealis* L. etc. In the thick moss-carpet a good deal of *Sphagnum*.—5.7.1966.

12. Skåne province (Scania), Hov parish, Knösen, 800 m NE bench mark 108. Talus from the NE-facing escarpment of acid gneiss, with beechwood. Intermixture of birch, rowan, *Prunus avium* L. Very rich litter, sparse vegetation of *Geranium robertianum*, *Oxalis acetosella*, *Dryopteris filix-mas*, *Athyrium filix-femina*, raspberry. Patches of mosses on boulders. Below more scattered boulders, mainly bilberry and *Oxalis*.—14.10.1970.

13. Västergötland province, Vänersnäs parish, Munkesten, 900 m ESE of the crossroad, on



the N slope of the Hunneberg table-mountain. Rather like loc. 9: a mossy boulder talus below a dolerite precipice, but lower, more damp and shady. Dominating *Salix caprea*, intermixture of linden, rowan, elm, birch and hazel. Rather sparse field layer mainly of ferns: *Dryopteris dilatata* (Hoffm.) A. Gray, *D. filix-mas*, *D. spinulosa*, *Polypodium vulgare*, also raspberry, *Impatiens noli-tangere*, *Geranium robertianum*, *Oxalis acetosella*. At the foot of the precipice *Calamagrostis arundinacea*, here also small springs and water trickling over shale screes. In the light parts with open tree stands a denser field layer, also nettles and *Lonicera xylosteum*.—18.8.1963.

14. Västergötland province, Brunn parish, the N slope of the hill Kråkeboberg. Diorite in the upper part, gneiss below. Luxuriant wood on the moss-covered boulder talus. Beech, linden, spruce, hazel, with more scattered maple, elm, birch and oak. Rather rich field layer of various grasses, *Anemone nemorosa* and *A. hepatica*, *Oxalis acetosella*, raspberry, *Dryopteris spinulosa*; in the lower part also *Mercurialis perennis* and *Aegopodium podagraria* L.—3.7.1963.

15. Dalsland province, Änimskog parish, 900 m SSE of Sikerud. Old linden wood on steep NE-slope of a high quartzite ridge. In the upper part stone taluses, further down a phyllitic slope with more scattered boulders. Intermixture of spruce, some hazel, *Salix caprea*, maple, elm, *Lonicera xylosteum*. Dominating *Festuca altissima* All., *Oxalis acetosella* and *Galium odoratum* (L.) Scop., varying intermixture of *Matteucia struthiopteris* (L.) Tod., *Dryopteris filix-mas*, *Lastrea dryopteris*, *Anemone hepatica*, *Lathyrus vernus* (L.) Bernh., *Cardamine bulbifera* (L.) Cr., *Actaea spicata*, *Milium effusum* L. etc. Rather mossy, mainly *Rhytidiadelphus triquetrus* and *Plagiothecium undulatum* (L.) Br.—29.9.1967.

### 13. ON CAUSES OF HIGH DIVERSITY, WITH SOME CONCLUDING REMARKS

The relatively high diversity in wooded boulder slope habitats in SW Sweden should be seen against the following background.

In all 64<sup>2</sup> species of snails and 18 species of slugs are known from the surveyed area. As shown in section 7, of these, 49 snail and 14 slug species have been recorded from boulder slope habitats. The others are throughout pronounced hygrophiles, synanthropes or calciphilous meadow species.

For reasons considered in section 10, not all these could be expected to co-exist in the same gross habitat. In the present material up to 34 snail species and 7 slugs (these, however, not in the same site as the richest snail community) have been found together. From certain considerations (Section 10) it is estimated that 37 snail species may co-exist in the most favourable sites.

Calculated on the actual number of species recorded this corresponds to 47.6% of the total terrestrial mollusc fauna of the area; calculated on the expected number, to 53.7%. This must be considered as a fairly high proportion.

We are still very far from the requisite knowledge of population dynamics, niche specialization, innate reproductive capacity and eliminative factors to give a causal explanation for this high degree of co-existence among terrestrial molluscs. Therefore, remarks can be given in rather general terms only, perhaps useful as hints to further research.

It seems reasonable to explain the high—absolute and relative—diversity in the first place by the following causes and conditions.

(a) The geographical situation on the sea-wind exposed side of the continental land-mass is

<sup>2</sup> Of these *Acicula polita* (Hartmann) is now seemingly extinct.



generally favourable for the development of a rich land mollusc fauna. Rainfall is adequate, thermoclimate mitigated. There are several similar examples from other parts of the world. Specific for NW Europe is the influence of the Gulf Stream, resulting in higher winter temperatures than elsewhere at corresponding latitudes (*c.* 58°).

(b) Access to calcium carbonate, or generally a high degree of eutrophy, favours the mollusc fauna, but cannot be considered a primary cause in the present context. As shown in this paper a fairly high diversity can occur also in an entirely non-calcareous environment. Wäreborn (1969, tables 7–10) has shown that even demanding species (such as *Columella edentula*, *Aegopinella nitidula*, *Macrogastra plicatula* and *Bradybaena fruticum*) occur at a fairly low content of calcium, in the form of organic compounds in the litter, of under 0.9%. This should be seen in relation to the fact that the lowest calcium value in Wäreborn's material, stated to be from a highly oligotrophic coniferous wood, was 0.51%.

(c) The rich microhabitat differentiation which is a constituent of the wooded talus and boulder slope habitats (*cf.* section 6).

(d) Most of the species which constitute the fauna show a relatively low degree of ecological specialization. This is shown by a rough, arbitrary grouping of the 63 species recorded from wooded boulder slope habitats:

|                                                                         |    |
|-------------------------------------------------------------------------|----|
| almost exclusively woodland:                                            | 7  |
| tolerant woodland species, occurring in a wide range of other habitats: | 36 |
| catholic species:                                                       | 10 |
| non-woodland species, occasionally found in wooded boulder slopes:      | 10 |

Except for the catholic species, there is within the groups variation in ecological tolerance between species with regard to different factors. There is, however, a clear pattern in the occurrence of the species, which, with some generalization, can be expressed in the following way. There are groups of related species (e.g. clausiliids, *Vertigo* spp.) which have a basically similar ecology, though varying in their ecological tolerance. When conditions improve further species of the group tend to be added, until the 'full set' is present. Tables 3 and 4 give examples of this trend. It should be noted that this generalization is valid also on a microhabitat level: the assemblage of species may be found under the bark of the same log, or in the same handful of litter.

(e) The modest degree of ecological specialization is usually linked to wide geographical distribution. It seems reasonable to assume a common evolutionary background, referring to the Pleistocene history. Too highly specialized species were unable to survive the great and repeated climatic changes. Less specialized species had an advantage not only in survival, but also in establishing themselves in new habitats.

A consequence of this is that most of the species of the region can be regarded as pre-adapted to a broad ecological coexistence.

(f) The trend that species with similar ecology tend to accumulate, rather than replace each other when conditions become optimal, implies that inter-group competition is negligible. Boycott (1934) already came to the conclusion that competition is not a limiting factor for land molluscs, except in certain extreme habitats, 'austere and limited in possibilities'. Published evidence, so extensive that literature references might be superfluous, corroborates that this may be almost generally valid for woodland communities in central and northern Europe.

(g) However, against this view, it can be argued that under the apparent pattern of ecological distribution, suggesting a low degree of specialization and competition, a more subtle pattern of niche specialization may exist. Cameron (1978) found clear and consistent differences in activity pattern between species which, when resting, occur virtually mixed.



However, these differences relate to the groups of species with basically similar ecology, considered here under (d), rather than to the species within such groups. A plausible cause may be differences in food preference. Field observations suggest that a more diversified litter favours the coexistence of related species (e.g. of *Vertigo*).

To conclude, the major factors determining the high diversity of mollusc communities in the region seem to be macroecological conditions, which generally favour the mollusc fauna, rich microhabitat differentiation in the sites, the broad and overlapping ecological range of most species, and a probably low or negligible competition between the mollusc species.

#### 14. ON CAUSES OF DEFICIENCY IN DIVERSITY

Even if the causes of high diversity form the main subject of the present study, some attention must be devoted to cases when diversity is considerably lower than would be expected.

A low degree of microhabitat diversity is certainly a major cause of an unexpectedly poor fauna. A close examination of a habitat often will make apparent why it is unsuitable for particular species.

For the area surveyed, however, human impact on habitats may be a more important reason. Tree cutting, trampling, and other mechanical encroachments and subsequent changes in sun and wind exposure, litter accumulation etc. effectively eliminate microhabitats for stenotopic species. Vegetation may then recover, but the ecological niches for the species concerned remain empty. Indeed, as considered in section 6, the boulder topography offers the mollusc community a particularly good chance to survive periods of adverse conditions, and therefore elimination first hits species with a narrow, specialized ecology, usually more or less on the margin of their distribution. Absence of such species, in spite of seemingly suitable conditions, may be taken as an indication of grave disturbance of the habitat in the past.

However, also in this connection it must be stressed that the absence of species in samples does not necessarily imply that they are not present in the locality. Trends in the development of habitats, manifested by tree growth and succession, may alter which species are perceptible, without necessarily affecting their presence. A definite answer as to whether or not an abnormally low diversity is a reality can, therefore, be given only after extended sampling—in some cases over several years.

It should also be noted that, so far as talus and boulder slope habitats in SW Sweden are concerned, alteration of the habitats by human impact is followed only to a marginal extent, or in most cases not at all, by the establishment of synanthropic species. The original character of the mollusc fauna remains unaltered, as far as the species of which it is composed is concerned. The impact is almost invariably expressed as a shift in the relative abundance of species, as well as reduced diversity, without a more or less synanthropic element replacing the original species of the mollusc community.

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# NEW SPECIES OF *FUSINUS* (*SINISTRALIA*) AND *BULLIA* FROM MASIRAH, OMAN (PROSOBRANCHIA: BUCCINACEA)

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*Abstract:* This paper describes two new species based on material collected from localities along the east coast of the island of Masirah, Oman. No living specimens were found of either species and thus the descriptions are based on shell characters alone. The first is a sinistral whelk, *Fusinus* (*Sinistralia*) *gallagheri* sp. nov., which was studied by both authors. The other species, *Bullia rogersi* sp. nov., was described by one of the authors only (K.R.S.).

## INTRODUCTION AND LOCALITIES

The shells which provided the material for this paper were found during two expeditions of the Royal Air Force Ornithological Society to the island of Masirah in 1976 and 1979; further material came from the collection of Dr. D. T. Bosch. Most of the specimens were sorted from beach debris, all of apparently recent origin, washed up along the strand-line. As both species of Buccinacea described in this paper were associated with other marine mollusc shells known to be living on this coast, and because the shells retained their colour, we consider it unlikely that they were reworked from Pleistocene raised beaches.

*Collecting localities* (from north to south, see Fig. 1).

Locality 1: Sandy beach from Ra's Qudufah to Ra's al Jazirah. 20° 41' N, 58° 45' E to 20° 35' N, 58° 46' E.

Locality 2: Rassier. 20° 32' N, 58° 57' E. A small exposed beach to the north of Ra's al Ya.

Locality 3: Ra's al Ya. 20° 31' N, 58° 48' E.

Locality 4: Haql. 20° 21' N, 58° 38' E.

Locality 5: Urf. 20° 18' N, 58° 36' E.

Locality 6: Ra's Kaydah. 20° 17' N, 58° 37' E.

## DESCRIPTION OF SPECIES

***Fusinus* (*Sinistralia*) *gallagheri* sp. nov.**

Shell solid, sinistral, comparatively elongate with spire less than half the total height. Shell height (type specimen) 16.0 mm, breadth 8.8 mm. Whorls 4-5, sutures shallow and indistinct. Siphonal canal short (3 mm) and oblique. Mouth pear-shaped, inner lip smooth and without



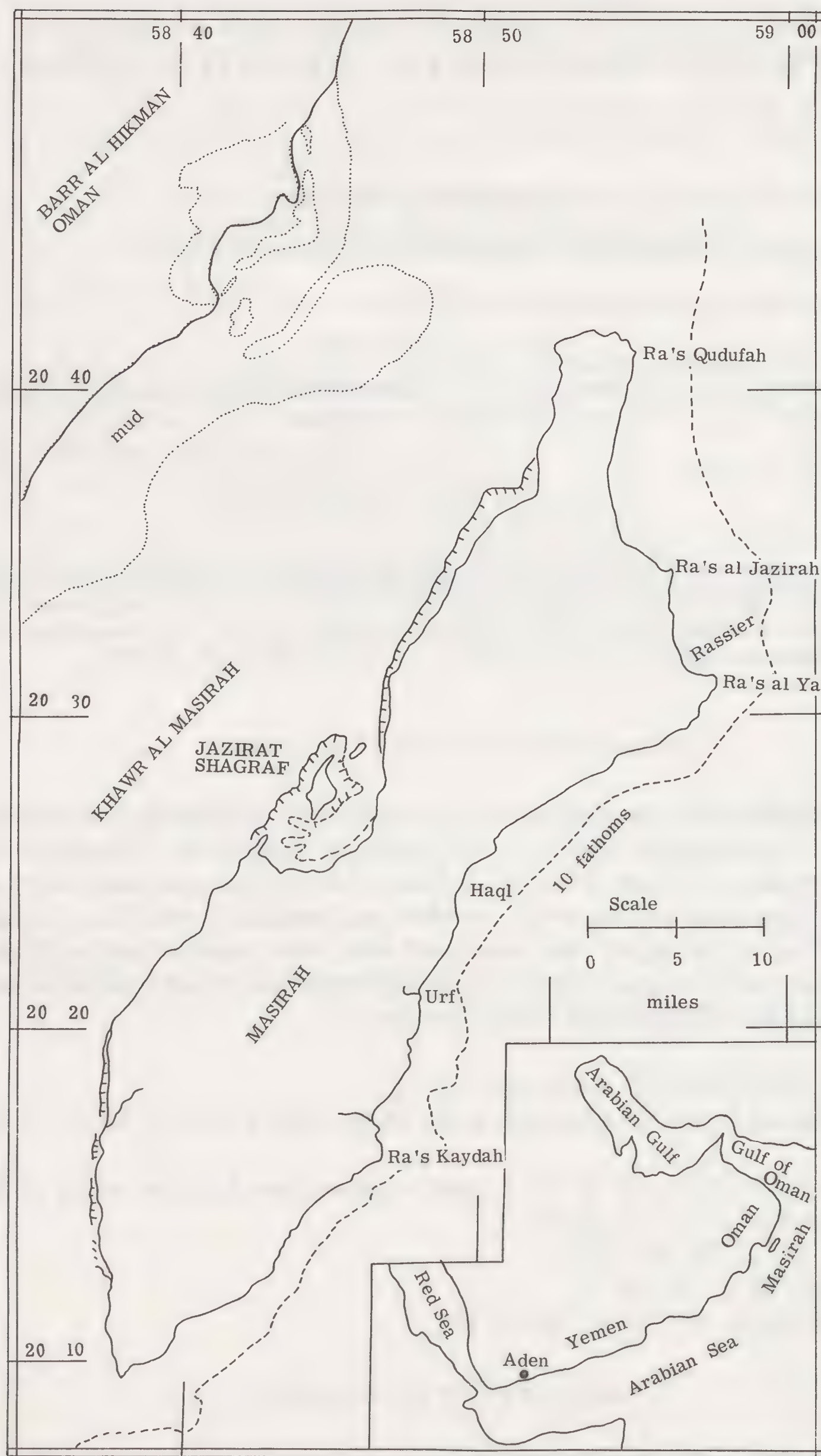


Fig. 1. Map of the island of Masirah, Oman, to show the position of collecting sites.



denticles. Sculpture consisting of distinct costae crossed by narrow spiral ridges, the costae bearing nodules at the periphery of each whorl. Body whorl with 7–8 costae and 12 spiral ridges. Protoconch smooth and colourless, followed by a teleoconch with regular brown axial ribs and no nodules. Shell dark brown with white markings, mostly at the tubercles.

Type locality: Rassier, Masirah, Oman. 20° 32' N, 58° 57' E.

Holotype: British Museum (Natural History), London. Registered number 198087. Height 16.0 mm, breadth 8.8 mm.

Paratypes: BM(NH) Registered number 198088. Height 19.6 mm, breadth 10.25 mm; National Museum of Wales, Cardiff. Accession number N.M.W.Z:1980:136.1–2. Height 14.6 mm, breadth 8.5 mm; height 18.6 mm, breadth 9.1 mm. A further paratype is deposited in the Zoologisch Museum, Universiteit van Amsterdam. The remaining material is in the collections of the authors and three shells in the possession of Dr. D. T. Bosch. (The latter specimens lack locality data, apart from 'east coast of Masirah'.) Specimens of this new species were found at all six localities listed. The dates of collecting and the numbers of shells are as follows:

Locality 1: 13 shells collected by T. D. Rogers in 1975 and 3 shells collected by M. C. Jennings on 20 November 1979.

Locality 2: Type locality. 1 shell collected by M. D. Gallagher on 24 October 1976.

Locality 3: 12 shells collected by T. D. Rogers in 1975.

Locality 4: 18 shells collected by T. D. Rogers in 1975.

Locality 5: 2 shells collected by T. D. Rogers in 1975.

Locality 6: 12 shells collected by T. D. Rogers in 1975.

#### *Related species*

*Fusinus* (*Sinistralia*) *gallagheri* differs from other species of the subgenus, *F.* (*S.*) *maroccensis* (Gmelin, 1791), *F.* (*S.*) *barclayi* (Sowerby, 1895) and *F.* (*S.*) *elegans* (Reeve, 1848), in the more solid nature of the shell, the shorter siphonal canal, usually greater breadth and the wide costae with peripheral nodules. In these characters it differs also from dextral members of the genus *Fusinus* (or *Fusus*). Shell ornamentation consisting of both spiral and axial elements is found in both dextral and sinistral species.

Although the small illustration of *Fusinus* (*Sinistralia*) *barclayi* in the original description (Sowerby, 1895) looks superficially like the species described in this paper, comparison with the type specimen in the British Museum (Natural History) showed that they were not the same. *F.* (*S.*) *barclayi* has a more delicate sculpture and has distinctly indented sutures which affect the profile of the spire. The costae are also less prominent.

*Sinistralia* was originally described as a subgenus by H. and A. Adams in 1853 with *Murex maroccensis* Gmelin, 1791 as the type species. None of the species of the subgenus *Sinistralia* are at all common and very little is known about their distribution, especially as some of the known specimens are without locality data. The two main areas, colonized by different species, are the north-west coast of Africa and the Canary Islands, and the north-east coast of Africa and the Arabian Sea; these two areas of distribution are separated by the Suez Canal. The most recently reported finds of *Sinistralia* are those of Saunders (1978) in the Canary Islands. East of Suez there is a record of a shell of *Fusinus* (*S.*) *barclayi* taken from Socotra, Arabian Sea, in 1919, which is in the Museum d'Histoire Naturelle, Paris.

To date, sixty seven shells of *Fusinus* (*Sinistralia*) *gallagheri* have been collected from the east coast beaches of Masirah, but all of these were dead shells and many were beachworn. In spite of subsequent searching on the shores of Masirah by Mr. M. D. Gallagher and Dr. D. T. Bosch, no live specimens have yet been located and it is probable that *F.* (*S.*) *gallagheri* lives off-shore in deep water and is only brought to the beaches occasionally by exceptionally rough seas.

Some of the shells had circular holes with bevelled edges (Plate 17b) and this is evidence of predation by another species of gastropod. Holes of this type are made by necklace shells



(Naticidae) and as these molluscs live in sand it suggests that *Fusinus* (*Sinistralia*) *gallagheri* may possibly be found on sandy bottoms off-shore.

***Bullia rogersi* sp. nov.**

Shell light in weight, whorls rounded, suture deeply incised and with a spiral cord below it, spire height slightly less than the total height of the shell, spire angle  $30^\circ$  and constant. Protoconch mammillate, smooth, translucent and glassy, the first whorl very small and scarcely raised above the next which is much larger and rounded. The first whorl of the teleoconch has five to six spiral grooves, the uppermost groove of the next whorl becoming much deeper and forming a strong spiral cord below the suture. This cord persists on all subsequent whorls but the other grooves weaken and disappear by the fifth whorl. There are up to eight whorls in all, with very weak growth lines (about forty on the body whorl) visible under magnification. The shell surface and the interior of the aperture are very glossy. The interior of the aperture is white to pale brown, the exterior ivory coloured with a pattern of numerous fine, wavy axial brown lines, some of which coalesce to form irregular brown blotches below the suture on the body whorl and on one or two of the preceding whorls. There are three to four very weak spiral grooves on the anterior part of the body whorl and up to six coarse cords on the fasciole, presenting a corrugated appearance. The columella is white; it has a weak terminal plait and there is a callus pad to the left of the columella in the parietal region in adult shells. The apical whorls are violet to indigo in 29 of the specimens examined, colourless in 6, and the remainder have the apices broken away.

Type locality: beach between Ra's Qudufah and Ra's al Jazirah.

Holotype: British Museum (Natural History), London. Registered number 198095. Height 20.50 mm, breadth 10.17 mm, aperture height 10.52 mm.

Paratypes: BM(NH): registered numbers 198096/1-4. Height of 198096/1 22.20 mm, breadth 10.60 mm, aperture 11.20 mm; 198096/2 height 20.70 mm, breadth 9.90 mm, aperture 10.20 mm; National Museum of Wales, Cardiff, accession number 1980.140.1. Height 20.52 mm, breadth 10.50 mm, aperture 11.50 mm (from type locality); collection of Dr. D. T. Bosch. Height 27.54 mm, breadth 13.45, aperture 14.00 mm. This is the largest specimen I have seen. Paratypes are also deposited in the Zoologisch Museum, Universiteit van Amsterdam and the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

*Bullia* was originally described as a genus by Griffiths and Pidgeon in 1834 with *Bullia semiplicata* Gray, 1839 as the type species. Specimens of this new species were found at only three of the localities listed above. The dates of collecting and numbers found are:

Locality 1: 27 shells collected by T. D. Rogers, 5 November, 1975; 21 specimens collected by M. C. Jennings on 20 November, 1979 (type locality).

Locality 3: 4 shells collected by T. D. Rogers, 19 September, 1975.

Locality 4: 4 shells collected by T. D. Rogers, 19 September, 1975.

Locality unknown: 14 shells collected by Dr. D. T. Bosch (all east coast beaches).

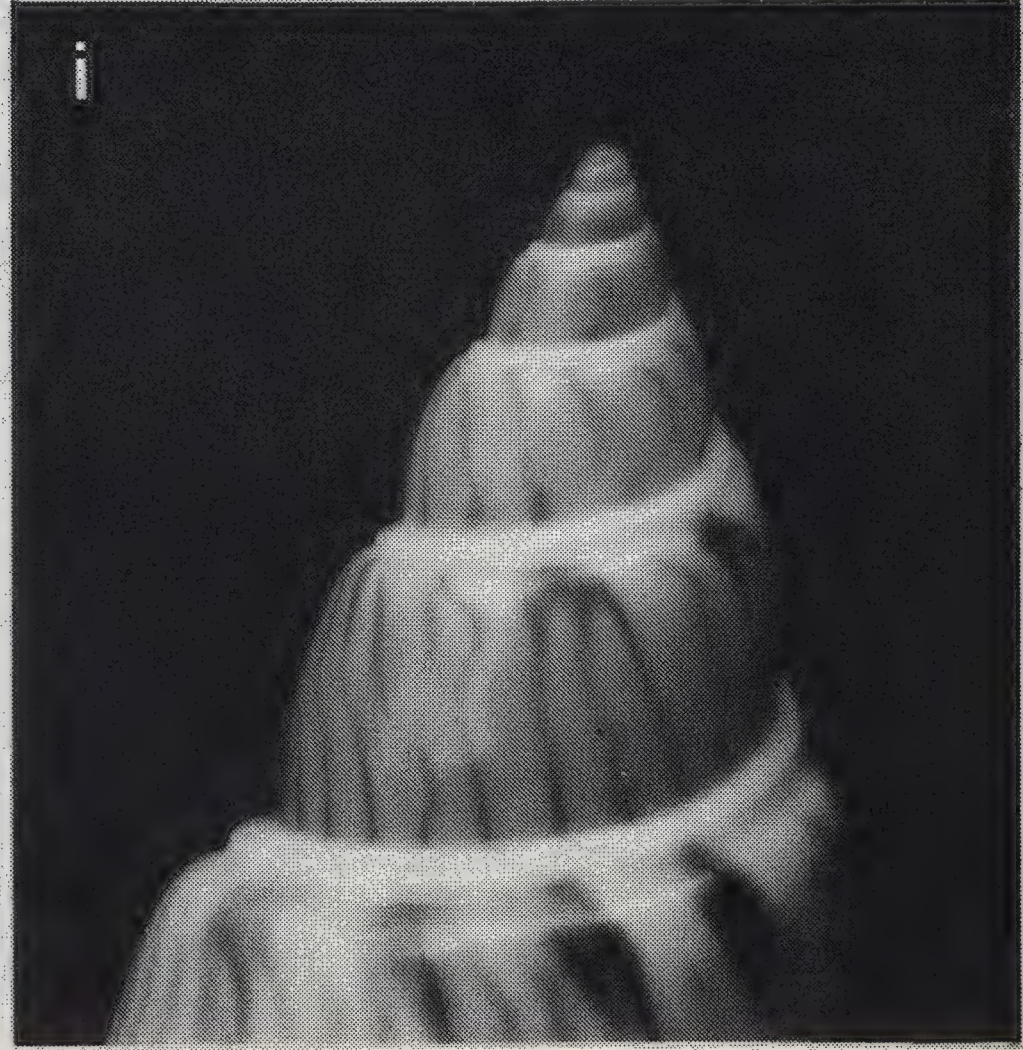
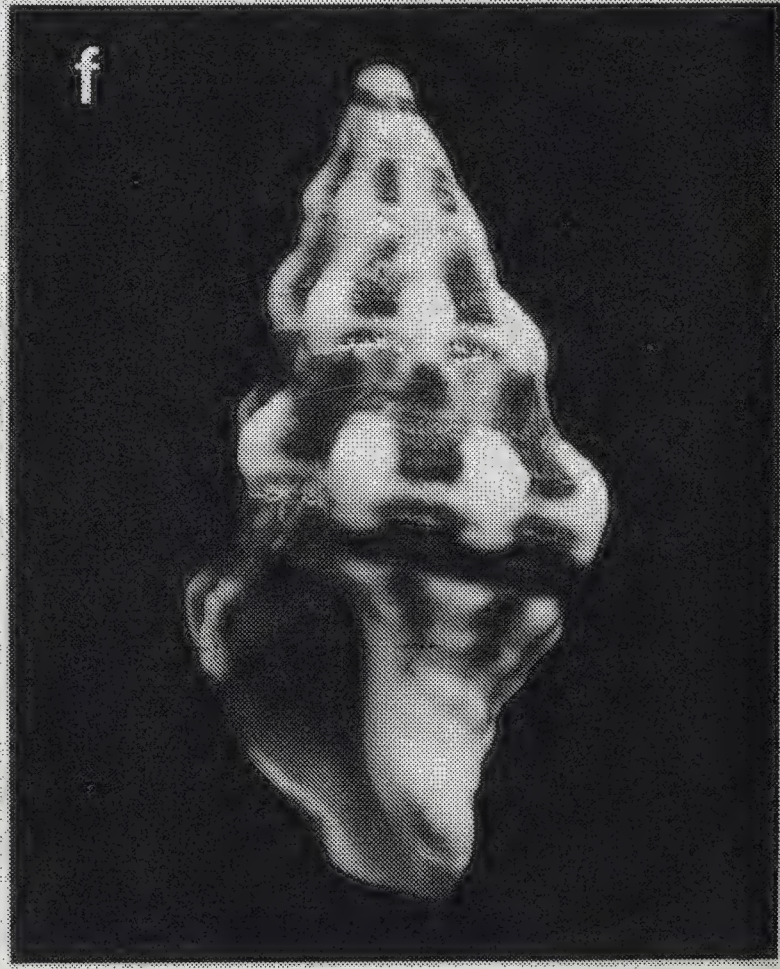
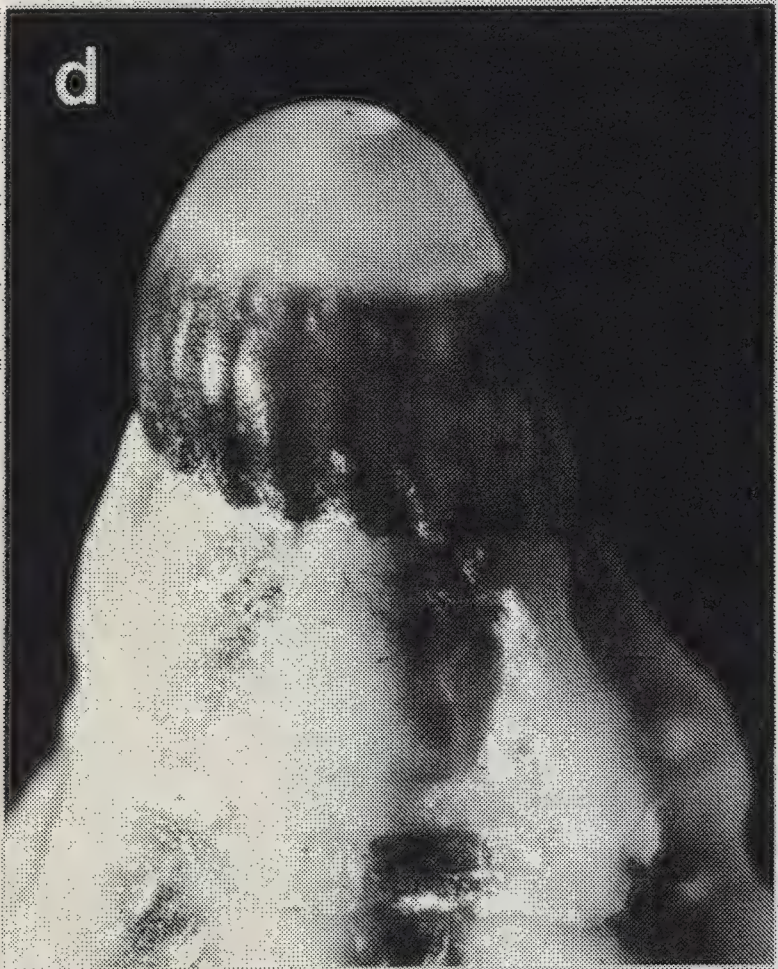
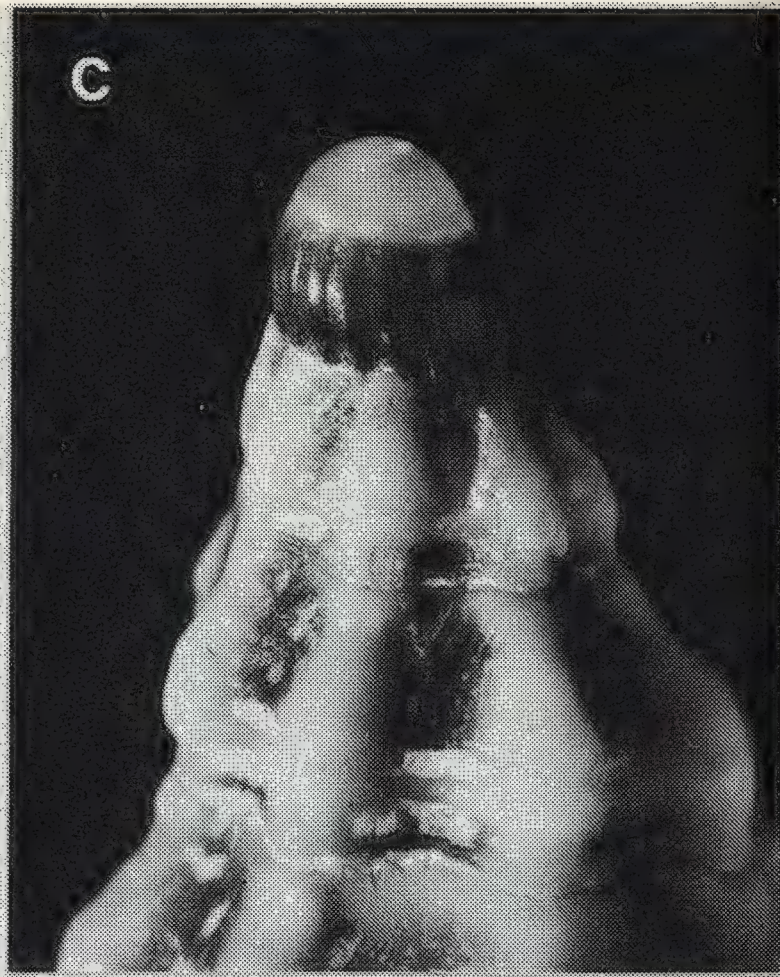
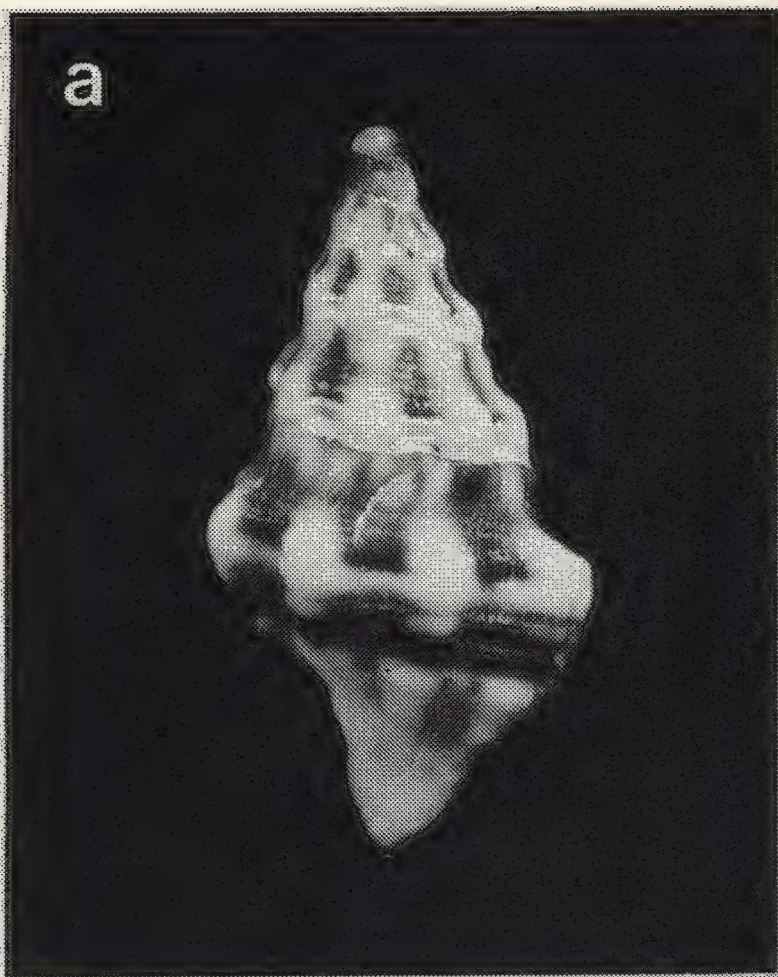
*Related species*

*Bullia rogersi* is similar in shape to the widespread *Bullia tranquebarica* (Roeding, 1798) and to *Bullia tahitensis* (Gmelin, 1791) which is fairly uncommon; both species occur in the Gulf of Oman and the Arabian Sea. *B. tahitensis* is sculptured with very strong rounded spiral cords and is much larger. In *B. tranquebarica* violet to indigo apices are very uncommon; the sub-sutural brown blotches are lacking and not all specimens are patterned with axial brown lines; the apical grooves are weak, become deeper on the later whorls and persist on all whorls; the grooves on the fasciole are few and very coarse and the callus pad on the columella is very weak or lacking.











None of the specimens examined showed signs of having been attacked by predators such as *Natica* spp. and all were washed up on the beach dead or inhabited by hermit crabs.

#### ACKNOWLEDGEMENTS

The authors are grateful to Mr. M. D. Gallagher and Mr. T. D. Rogers who brought the two new species to our attention; Mr. Rogers also collected the bulk of the material. Other specimens were collected by Mr. M. C. Jennings, and Dr. Donald T. Bosch of Muscat made his specimens available to us for study. Shells of *Sinistralia* were made available for comparative study from the Museum d'Histoire Naturelle, Paris, the Academy of Natural Sciences, Philadelphia, and Mrs. Celia Pain. We are deeply indebted to Mr. C. P. Nuttall of the BMNH for his generous help with *Bullia*, to the staff of the Mollusca Section of the BMNH for help and museum facilities, and to Professor A. Graham. Some study was undertaken in the Zoology Department of the National Museum of Wales. The photographs of *Sinistralia* were taken by Mr. E. Broadbent of the NMW. The expeditions on which the shells were collected were made possible by special permission of His Majesty Sultan Qaboos bin Said.

#### REFERENCES

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 GRIFFITHS, E. and PIDGEON, E., 1834. *The Mollusca and Radiata arranged by Baron Cuvier with supplementary additions to each order*. 601 pp. London.  
 SAUNDERS, G. D., 1978. Sinistral *Fusinus* from Lanzarote (Canary Islands). *La Conchiglia* No. 110–111: 18–19.  
 SOWERBY, G. B., 1895. Descriptions of twelve new species, chiefly from Mauritius. *Proc. malac. Soc. Lond.* 1: 41–44, pl. 4.

*Note.* Since this paper was written, live specimens of both *Fusinus* (*Sinistralia*) *gallagheri* and *Bullia rogersi* have been collected from Masirah by one of the Authors (K.R.S.) Work on these is now in progress.

PLATE 17. a–f. *Fusinus* (*Sinistralia*) *gallagheri* sp. nov. a–d, holotype, British Museum (Natural History); e–f, paratype, National Museum of Wales. Dorsal and ventral views and apex. g–i. *Bullia rogersi* sp. nov. Holotype, British Museum (Natural History). Dorsal and ventral views and apex. a, b, e, f, x3; c x12; d x18; g, h x2; i x5.



## REVIEWS

*A Collectors Guide to Seashells of the World.* By Jerome M. Eisenberg. Published by McGraw-Hill Book Company, 1981. ISBN 0 07 0191409. Price £12.95. 239 pp., including 158 colour plates.

The book consists of an introduction in the first 29 pages which also include 12 colour plates illustrating a variety of shell forms. This is followed by the bulk of the plates (13-158) and these by the main text (pp. 177-219) and index.

The aim of this book, stated by the author, is to illustrate all the seashells which might commonly be met with on the shore or on the dealers' shelves. To this end he has selected some 2,600 species. It is thus a book for the beginner or casual collector rather than the specialist and must be criticised or appraised in this context. The essence of the book is plates 13-158 which illustrate the shells, grouped according to families. I tested the author's selection of species by identifying a number of common Caribbean and British shells by reference to the plates only, without reading the text. I was very satisfied with the results.

The quality of the plates is fair. Each family is shown against a different coloured background and I found this to be obtrusive in many cases, particularly when a red shade was the background colour. Multiple light sources have been used for photography (usually one from the left and right sides of the shell) which cause multiple shadows leading to a confusing background and also a rather flat image; the shadows are intentional (implied on page 219) but I do not like them. However, there has been a great deal of thought put into the selection of shells and the preparation of plates, by the author, and this overrides my criticism of them. In those cases where a number of families are illustrated on one plate the different coloured backgrounds separate them at a glance. Moreover, in each family the shells are illustrated at one magnification (mostly full-size or at x2/3) so that different sized species can be compared. In a few cases this has resulted in untypically small shells having been chosen for illustration and where a large and small shell are illustrated together there is some loss of clarity due to focusing difficulties. With the Patellidae and Haliotidae it is not made clear that most of the illustrations are of the inside of the shell, but this is unlikely to lead to confusion. Below each plate are the names of the shells (with authors) the common names, distributions, size ranges and variations.

The introduction is short. Useful here is the description of the marine zoogeographical regions, supplemented by a map. The text gives a very brief account of the characteristics and distribution of the families with a crude line drawing of a typical member of the family. A glossary of terms and bibliography follow. A list of societies is given but this lacks full addresses except in the case of United States societies. The author suggests that the collector contacts the relevant museum for this information but the museum addresses are also incomplete. Under England are listed the British Museum (Natural History) with the address given as London and the National Museum of Wales!

Is there a need for another shell book? Perhaps not, but this book accomplishes its author's intentions well. It is a book for working from, not a 'coffee-table' book. The layout makes it very easy to use, it is well bound and considering the number of plates, reasonably priced.

B. COLES.

*Slizni fauny SSSR i sopredelnykh stran (Gastropoda terrestria nuda)* [The fauna of the slugs of the USSR and adjacent countries]. By I. M. Likharev and A. Wiktor, in *Fauna SSSR, Molljuzki*, vol. III., part 5, 438 pp., 576 figs., 1 colour plate. 'Nauka', Leningrad, 1980. Price 6,60 roubles.

Great credit for studying the slugs of Russia must go to H. Simroth (1851-1917). His most significant monographic study is *Die Nacktschnecken des Russischen Reiches* (321 pp., St. Petersburg, 1901). In this work he already paid attention to anatomy. Furthermore he also wrote important studies on the slugs of the Caucasus and central Asia. P. Hesse (1926), using Simroth's studies, put together a classification of slugs to which most research has adhered until now.

The very attractive book written by the prominent specialists I. M. Likharev and A. Wiktor represents an excellent monograph of the slugs occurring in the territory of the Soviet Union and adjacent countries, i.e. Finland, Poland, Czechoslovakia, Romania, Hungary, Turkey, Iran, Afghanistan, Mongolia, and also of the adjacent provinces of China and Korea. The slugs of the Balkan peninsula, of the western and southern parts of Europe and of north Africa have not been included.

The book consists of the following parts: first there is a systematic survey of the species, and then a general part devoted to morphology and to basic aspects of physiology (morphology, anatomy, reproduction and ontogeny). Later chapters deal with food, environment, parallel evolution, systematic position and phylogeny of individual families, geographical distribution, synanthropic and anthropochorous species, economic importance, methods of slug control and techniques of study (collecting, culturing, preserving, dissection). Three-quarters of the book are occupied by the systematic part. The classification has been arranged in a rather different way to that we are familiar with, especially as regards the position of the superfamily Arionoidea. The authors present a new superfamily classification, viz. 1



## REVIEWS

Limacoidea (Agriolimacidae, Boettgerillidae, Limacidae), 2 Trigonochlamydoidea (Trigonochlamydidae), 3 Zonitoidea (Parmacellidae, Milacidae), 4 Arionoidea (Philomycidae, Arionidae).

The descriptions of individual species are based upon rich collections, revisions of type specimens, etc.

For each species the following data have been given: synonyms, type locality, investigated material (number of specimens and their origin), description of the animal (habitat, dimensions, shell, radula), anatomical characters (with illustrations to each species), distribution, way of life, and, if necessary, other remarks.

The book also includes keys to families, genera and species.

From the territory under investigation, 102 species belonging to 29 genera and 8 families are given. The most varied fauna rich in endemic species and genera has proved to be in the Caucasus and in the neighbouring mountainous territories of Turkey and Iran. Another, smaller centre of endemics lies in the mountainous region of central Asia.

The systematics both of species and of higher units have been radically altered here, if compared with former opinions. According to the most recent previous monograph (Likharev and Rammelmejer, 1951), 125 slug species belonging to 23 genera were given from the territory of the USSR. Now 68 species and 3 genera of that list are regarded as synonyms! At the present time, 70 species belonging to 27 genera are given from the territory of the Soviet Union (12 of these species are new to the fauna of the USSR and 3 species are new to science). The authors do not believe that investigation of this territory has finished, especially with respect to the immense areas of Siberia and central Asia which remain insufficiently explored. The book closes with 488 references to literature quoted.

As a whole, the reviewed book can be characterized as a unique monograph of the slugs of the territory concerned (i.e. a substantial part of palaearctic region) and will serve as an indispensable manual to students dealing with this animal group. Even to those who are unacquainted with the Russian language this work is understandable owing to the many (576) excellent line drawings (originals, or taken from other sources) made by Mrs. N. N. Frunzeeva.

IVO FLASAR

*Pulmonates*. Vera Fretter and J. Peake (editors). *Volume 2A Systematics, Evolution and Ecology* (1978) pp. xi, 540. *Volume 2B Economic Malacology with particular reference to Achatina fulica* (1979) pp. x, 150. Academic Press, London, New York and San Francisco.

The first volume of this series (Functional Anatomy and Physiology) appeared in 1975, and papers in volume 2A have notes that the mss were delivered in 1972, or submitted in 1972 and returned for hasty correction in 1977, or submitted in 1975, etc.; similarly volume 2B contains no reference later than 1976—there seems to have been some delay in the publication. Nevertheless, these are two very useful volumes. The chapters of the first (2A) are: Systematics and comparative morphology of the Basommatophora (B. Hubendick); Classification of the land Mollusca (A. Solem); Experimental methods in molluscan systematics (G. M. Davis); Chromosomes of pulmonate molluscs (C. M. Patterson and J. B. Burch); Genetic variation and natural selection in pulmonate molluscs (B. Clarke, W. Arthur, D. T. Horsley and D. T. Parkin); Slugs—a study in applied ecology (P. J. Hunter); Pulmonate molluscs as intermediate hosts for digenetic trematodes (D. S. Brown); Ecology of freshwater pulmonates (W. D. Russell-Hunter); On the evolution of gastropods in ancient lakes (K. J. Boss); Distribution and ecology of the Stylommatophora (J. Peake). The second volume (2B) is a single treatise by A. R. Meade in 10 chapters, with an extensive reference list and subject index, on the so-called Giant African Snail *Achatina fulica*.

Proofreading is not always meticulous (one chapter of Meade's treatise is omitted from the 'Contents of Volume 2B' in vol. 2A, and there are some rather remarkable misprints) and editing is rather uneven. Some authors should have been told that sentences are separated by more than a comma, and odd remarks beginning with 'Particularly as . . .' or similar phrases are not separate sentences. Moreover, inverted commas should never be used in scientific prose except to mark an actual quotation, or perhaps to introduce a new term (in which case italics are better). Any other use only serves to warn the reader that the author does not mean quite what he says, without saying what he does mean. This is useless even to English-speakers, and a real menace to a non-English-speaker, perhaps painfully translating a particular paragraph with a dictionary. Scientific English should be less idiomatic than spoken or literary English, entirely without silly trendy phrases (including slang) which may need a special dictionary in ten years' time, and as plain and expressive as possible. Some of the articles come up to these standards; a few do not.

The two volumes could perhaps have been better constituted if the more applied or medically oriented papers (on slugs and intermediate hosts) in 2A had been placed in 2B, but this is very much a matter of taste. It is impossible in this review to comment in detail on the various contributions (and I am not competent to do so for several). It is always possible to disagree with a few points here and there, but that is not really helpful to anyone. There is a fine diversity of subjects, written by workers of reputation, and even though the reference-lists are now somewhat out of date, the volumes are essential for anyone interested in pulmonates in whatever way.

A. J. CAIN



# PROCEEDINGS OF THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

## TREASURER'S REPORT, 1980

In spite of the fact that the annual subscription was increased in 1980 the accounts show a deficit of £1,319.05. This, however, is somewhat misleading since the major part of the deficit was incurred in 1979, but was masked by the Royal Society's grant of £1,000 towards the publication of *Special Publication* No. 1. The true reason for the deficit was that the 1980 increase was too little and too late. Additionally, the *Special Publication* proved to be considerably more expensive than had been anticipated, but since it was very well received it may be hoped that the loss on this may to some extent be made up by the sale of copies still remaining in hand.

The income from the Members' subscriptions and from *Journal* subscribers cannot be compared with that for 1979 because of the increases; other items of income remain fairly similar.

The chief items of expenditure were, as always, printing and postage, and as usual these have increased. It should be mentioned that the increase shown under 'Printing, Stationery and Postage' is disproportionately large, since it includes postage on two additional publications: Dr. T. Gascoigne's *Fine dissection of Ascoglossans* and Dr. M. P. Kerney's *Conservation of snails, slugs and freshwater mussels*. Our thanks are due to Dr. Gascoigne and to the Nature Conservancy Council respectively for supplying the Society free of charge with copies for all Members. Another item which as usual is included under this heading is the annual Members' List: as the cost of this is now in the region of £500 it has been decided as an economy measure that this will be issued less frequently.

In view of very much increased postage, increased rent for the meeting room and anticipated higher printing costs the Council has reluctantly been obliged to recommend another increase in subscriptions to take effect in 1982; proposals were included in the agenda for the Special General Meeting.

26 Ordinary Members and 3 Junior Members are in arrears with 1980 subscriptions. No further publications can be sent in 1981 to any Members whose current subscriptions remain unpaid, although any which have been withheld will be sent upon receipt of the subscriptions. In view of the very heavy cost of posting reminders Members are urged to check that their subscriptions are paid, and that any bankers' orders are for the correct amount.

Covenanted subscriptions produce useful additional income, and the Society will be grateful to any Members who are prepared to pay their subscriptions in this way.

MARJORIE FOGAN  
*Hon. Treasurer*

## REPORT OF THE COUNCIL 1980-81

It is with regret that the Society has to report the deaths of the following 7 members, an unusually large number: G. A. S. Barnacle, V. A. G. Brown, G. E. Crisp, Mrs. M. Hill, G. B. Mitchell, J. L. Newton and C. Swanesveld.

*Membership.* The membership now stands at 602 Members comprised of the following categories: Full Members 498; (Full Life Members 36); Family Members 29; (Family Life Members 8); Honorary Members 3; Junior Members 28. During the year 23 Members resigned, 29 were struck off for non payment of subscriptions and 52 new Members were elected.

*Subscribers.* There are approximately 200 subscribers to the *Journal of Conchology*. During 1980 there were 5 cancellations and 3 new subscribers.

*Meetings.* Seven ordinary meetings were held, in the Demonstration Room, British Museum, Natural History, as well as one Annual General Meeting.

*Publications.* Two parts of the *Journal of Conchology* were issued, Volume 30 parts 3 and 4. Four issues of the *Conchologist's Newsletter* were issued, also a programme card of events and a membership list. A revised edition of *Papers for Students* No. 7, *Guide to selected literature on British Mollusca* by Stella M. Turk, was printed. This is available for all members to purchase, but will not be issued free of charge to every member as it is not a new publication. The booklet *Fine Dissection* by T. Gascoigne was also issued free to all members by the kind offices of the author, whom we thank. The booklet had been published by the author with co-operation from the Society.



BALANCE SHEET AS AT 31st DECEMBER, 1980

|                                     |            |          |                                   |                  |
|-------------------------------------|------------|----------|-----------------------------------|------------------|
| Creditors and Accrued Charges . . . | £          |          |                                   | £                |
| Fees and Subscriptions in Advance   |            | 2,831.25 | Cash in hand . . . . .            | 23.00            |
| Life Membership Fund . . . . .      |            | 602.23   | Cash at Bank:—                    |                  |
| Reserve and Research Fund . . .     |            | 2,890.00 | Current Account . . . . .         | 2,414.05         |
|                                     |            | 1,561.50 | Deposit Account . . . . .         | 1,091.72         |
|                                     |            |          | Post Office Savings Bank . . .    | 3,299.42         |
|                                     |            |          |                                   | <hr/> 6,828.19   |
| <i>Capital Account</i>              |            |          |                                   |                  |
| Balance Brought Forward . . .       | 8,239.04   |          | Investments:—                     |                  |
| Less Deficit for the Year . . .     | (1,319.05) |          | £400 5% Treasury Stock 1986/89    | 344.00           |
|                                     | <hr/>      |          | £500 5¾% Debenture Stock, Mersey  |                  |
|                                     |            |          | Docks & Harbour Board 1980/82     | 222.29           |
|                                     |            |          | 2514 Units M. & G. Dividend Fund  | 1,522.06         |
|                                     |            |          | £400 12½% Loan City of Norwich    | 400.00           |
|                                     |            |          | £800 5½% Loan London County       |                  |
|                                     |            |          | Council . . . . .                 | 769.20           |
|                                     |            |          | 1620 Save and Prosper Units . . . | 892.95           |
|                                     |            |          | £875 Spillers 7% Debenture Stock  |                  |
|                                     |            |          | 1978/83 . . . . .                 | 753.82           |
|                                     |            |          | £700 Bury 12¼% Loan . . . . .     | 700.00           |
|                                     |            |          | £800 15½% Treasury Stock 1998     | 768.00           |
|                                     |            |          | £95.68 Subordinated Loan Stock—   |                  |
|                                     |            |          | Mersey Docks and Harbour Board    | 95.68            |
|                                     |            |          | 104 10p. Ordinary Shares, Mersey  |                  |
|                                     |            |          | Docks & Harbour Board . . .       | 10.40            |
|                                     |            |          | £2340 7¼% Whitbread Stock 1995/99 | 1,498.38         |
|                                     |            |          |                                   | <hr/> 7,976.78   |
|                                     |            |          |                                   | <hr/> £14,804.97 |

WM. F. EDWARDS  
L. LLOYD-EVANS

Hon. Auditors

11th March, 1981

MARJORIE FOGAN,  
Hon. Treasurer.



THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31st DECEMBER, 1980

|                                                 | £         | £        | £         |
|-------------------------------------------------|-----------|----------|-----------|
| Publications:                                   |           |          |           |
| News Letter . . . . .                           | ...       | 1,744.44 | ...       |
| Student Papers.. . . .                          | ...       | 28.80    | ...       |
| Special Publication . . . . .                   | ...       | 2,448.40 | ...       |
| 5,381.31                                        |           |          |           |
| 1,176.62                                        |           |          |           |
| Journal:                                        |           |          |           |
| Volume 30 No. 3 . . . . .                       | 2,343.21  |          | 132.11    |
| Volume 30 No. 4 . . . . .                       | 1,896.17  |          |           |
| Back Numbers . . . . .                          | 56.25     |          |           |
| 4,295.63                                        |           |          |           |
| Shell Kits . . . . .                            | 32.63     |          | 59.70     |
| Cost of Atlas, Postage and Packing . . . . .    | 17.18     |          | 31.22     |
| Printing, Stationery and Postage . . . . .      | 1,010.20  |          | 40.16     |
| Officers Expenses.. . . .                       | 189.21    |          | 59.06     |
| Subscriptions . . . . .                         | 7.00      |          | 45.24     |
| Meetings . . . . .                              | 105.40    |          | 26.50     |
| Book Markers . . . . .                          | 18.40     |          | 7.05      |
| Sundry Expenses . . . . .                       | 6.30      |          |           |
| 268.93                                          |           |          |           |
| Investment Income:—                             |           |          |           |
| General Account . . . . .                       | ...       | 1,203.44 | ...       |
| Life Members' Fund . . . . .                    | ...       | 422.13   | ...       |
| Reserve and Research Fund . . . . .             | ...       | 199.01   | ...       |
| 1,824.58                                        |           |          |           |
| Transfer to Reserve and Research Fund . . . . . | ...       | 199.01   | ...       |
| 1,625.57                                        |           |          |           |
| Net Surplus . . . . .                           | 9,903.59  |          | 8,584.54  |
| —                                               |           |          | 1,319.05  |
| Net Deficit . . . . .                           | £9,903.59 |          | £9,903.59 |



## PROCEEDINGS

*Change of Officer.* Dr. C. R. C. Paul asked to be relieved of his duties as Honorary Editor when he was granted a sabbatical year by Liverpool University. Dr. Paul had been a very good Editor and it was with a sense of shock that we received his resignation. In October Dr. B. Coles was appointed by the Council as 'Acting Honorary Editor', to be confirmed at the Annual General Meeting in March 1981.

*Field Meetings.* Four field meetings were held during 1980 as follows: April 26th–27th, Selborne, Hants. (Joint meeting with the Malacological Society). June 14th, East Suffolk (Joint meeting with the Ipswich Geological Group). July 20th, Northampton (Joint meeting with the Northampton N.H.S.). September 20th, Leicestershire. Two meetings were cancelled due to lack of support.

Thanks are due to the following for leading these meetings: Dr. J. E. Chatfield and Messrs R. A. D. Markham, A. G. H. Osborn and I. M. Evans.

*Change of subscription rates.* A special General Meeting was held on the 21st March 1981, immediately before the Annual General Meeting, to discuss the urgent need to raise subscriptions on January 1st 1982.

Introduction of the following subscription rates will come into force as from 1st January 1982:

Full Membership £10.00; Family Membership £12.00; Junior Membership £2.00; Corporate Membership £15.00; entrance fee £1.00.

It was also agreed that Life Membership and Family Life Membership would be discontinued forthwith.

## RECORDER'S REPORT: NON-MARINE MOLLUSCA

The following vice-county novelties have been verified since the last Report (*J. Conch., Lond.* **30**, p. 275). In all cases the date of collection was 1980–81.

Cornwall West (1): *Hippeutis complanatus*, Chiverton (10/7852), Mrs. S. M. Turk; *Testacella scutulum*, St. Ives (garden, 10/5140), J. Humphreys.

Somerset South (5): *Leiostyla anglica*, *Boettgerilla pallens*, Roadwater (31/0037), R. A. D. Cameron.

Hants North (12): *Milax sowerbyi*, Selborne (41/7433), R. C. Preece; *Boettgerilla pallens*, *Testacella scutulum*, The Wakes, Selborne (garden, 41/7433), Miss S. M. Davies and A. Norris.

Suffolk West (26): *Pisidium moitessierianum*, R. Stour, Long Melford (52/8543), I. J. Killeen.

Brecon (42): *Margaritifera margaritifera*, R. Wye, Hay-on-Wye (32/24), S. P. Dance.

Worcester (37): *Boettgerilla pallens*, Broadway (garden, 42/0936), P. Whitehead.

Caernarvon (49): *Boettgerilla pallens*, Crymlyn (23/6371), M. J. Ashdown.

Lincoln North (54): *Vertigo substriata*, Theddlethorpe (53/4791), Mrs. S. Barker.

Derby (57): *Boettgerilla pallens*, Hathersage (43/2380), R. Clinging.

York South-west (63): *Boettgerilla pallens*, Halifax (44/0424), Mrs. D. Shields.

Cheviot (68): *Hippeutis complanatus*, Detchant (46/0736), A. Walton.

Isle of Man (71): *Limax pseudoflavus*, Ballamaddrell (24/2571), S. H. P. Maddrell.

Kincardine (91): *Vertigo lilljeborgi*, Crathes Castle (37/7496), Mrs. D. K. Marriott.

Aberdeen South (92): *Hippeutis complanatus*, R. Don, Aberdeen (38/9309), M. B. Davidson.

Sutherland West (108): *Pisidium conventus*, Loch Mhaolach-coire (29/2719), D. H. Keen.

Clare (H. 9): *Vertigo pusilla*, Fermoyle (12/1704), D. T. Holyoak.

Few of the above call for special comment. The alien slug *Boettgerilla pallens* continues to spread, and was reported from six more vice-counties. *Vertigo pusilla* was found in the Burren country of Co. Clare, in mossy hazel scrub on a limestone pavement; this is only the second living find of this species in Ireland in the past thirty years.

M. P. KERNEY

## RECORDER'S REPORT: MARINE MOLLUSCA

Last year I reported the publication by Nature Conservancy Council for the Society, of species lists for each of the sea areas, and that I was using those species lists to draw distribution maps for all the species. My draft was completed at the end of 1980, and is now with NCC being prepared for publication later this year. The Atlas maps some 750 species, and includes a systematic list. I hope that it will stimulate increased interest in marine recording; it is intended to publish additions and amendments each year with the marine recorder's annual report. A list of sea area representatives was circulated with the Society membership list.

D. R. SEAWARD



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| Page                                            | Line |                                                      |
|-------------------------------------------------|------|------------------------------------------------------|
| 36                                              | 14   | for shaped read shaded.                              |
| 42                                              | 31   | for <i>Geol.</i> read <i>geol.</i>                   |
| 68                                              | 4    | for <i>castenea</i> read <i>castanea</i> .           |
| 72                                              | 10   | for <i>Trychycardium</i> read <i>Trachycardium</i> . |
| 250                                             | 13   | for Kabrak read Labral.                              |
| 277                                             | 12   | for Pilsbury read Pilsbry.                           |
| 309                                             | 3    | for <i>vigata</i> read <i>virgata</i> .              |
| Plate 16, Legend line 7 for Fig. 7 read Fig. 9. |      |                                                      |
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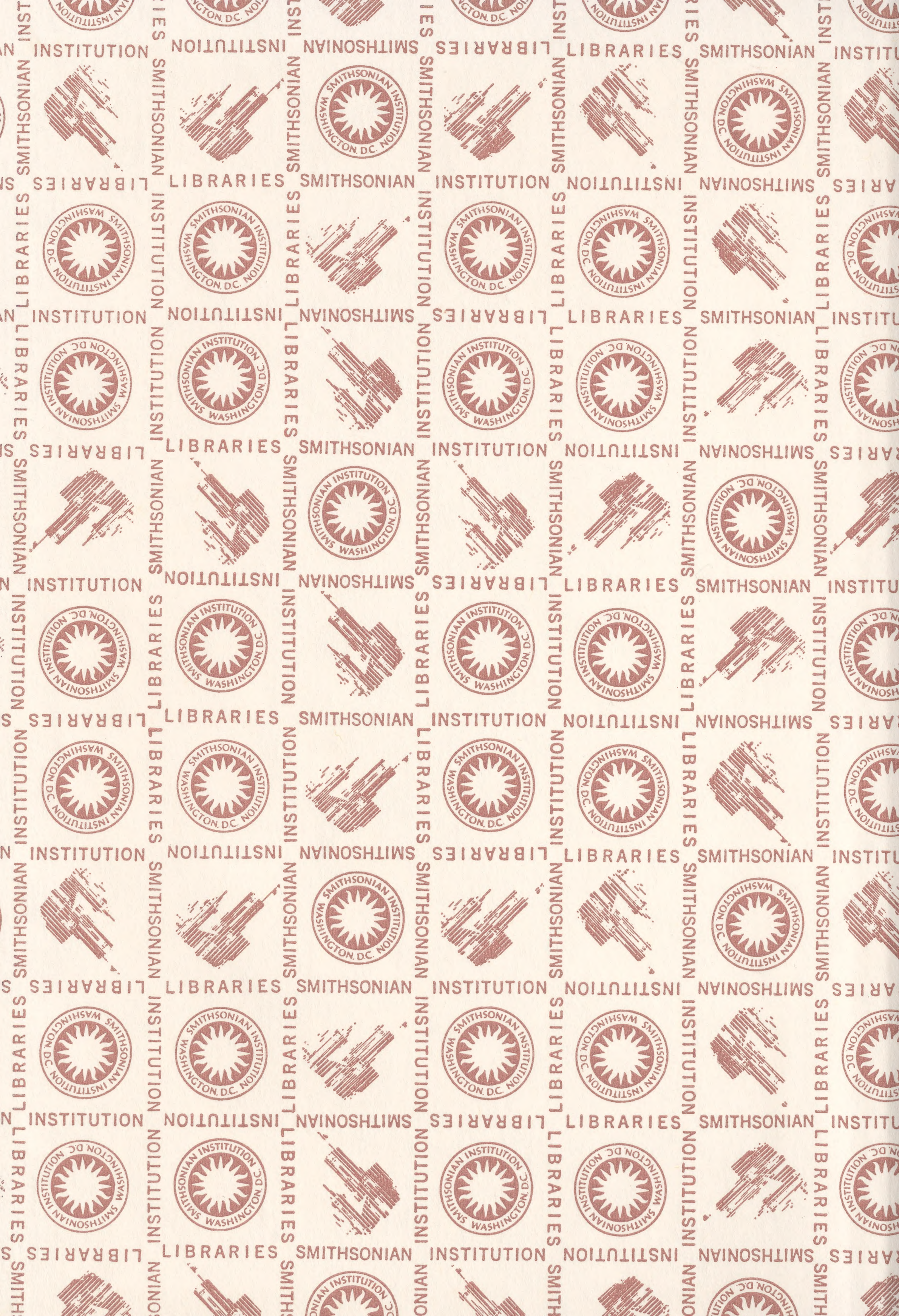




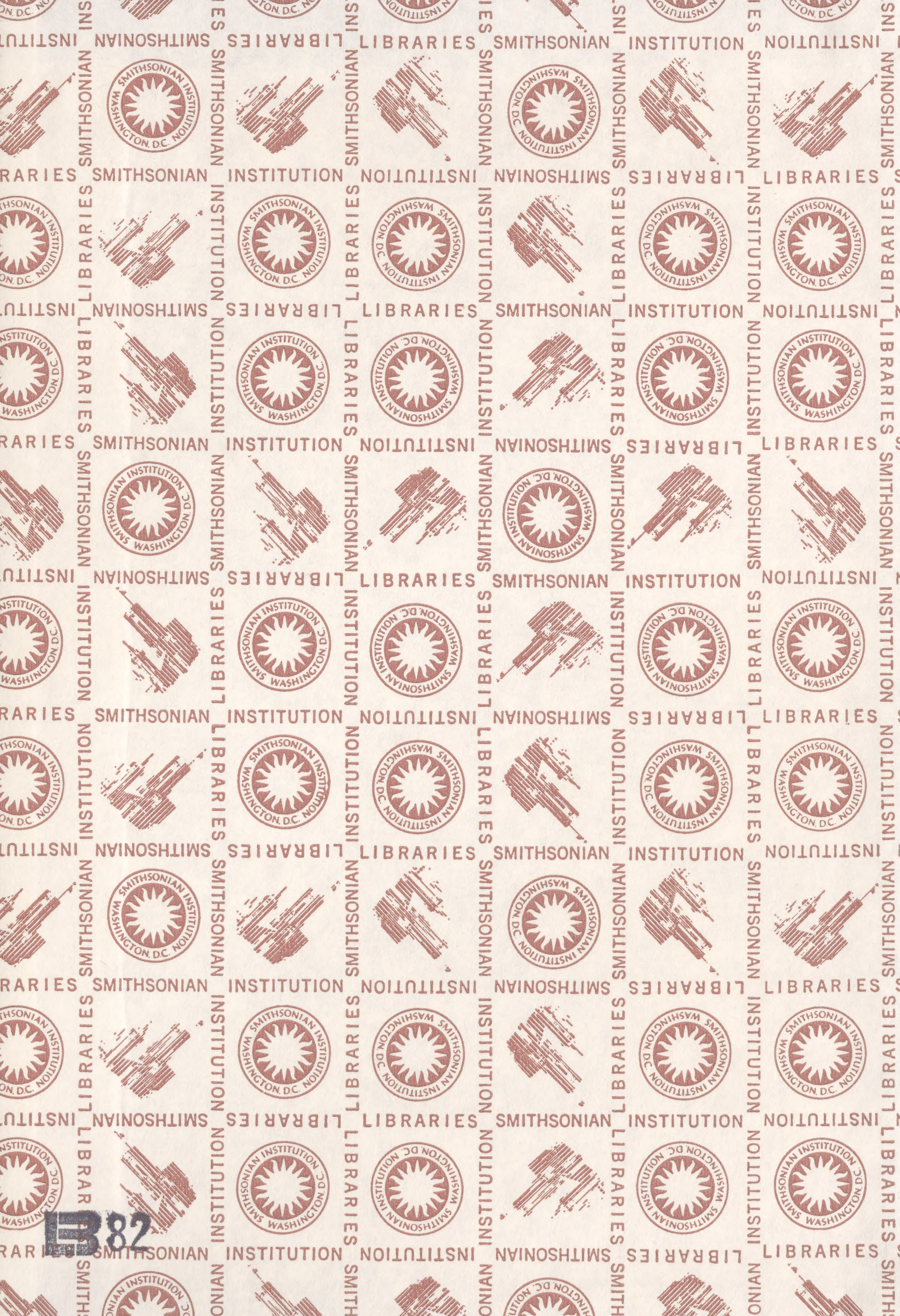












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